3

Current Status of Aquatic Ecosystems: Lakes

INTRODUCTION

Natural lakes that were suitable for occupation by suckers before land-use development and water management included Upper Klamath Lake, Lower Klamath Lake, Tule Lake, and Clear Lake (Figure 1-3). All of these lakes have been changed morphometrically and hydrologically and are now used in the Klamath Project water-management system for storing and routing water. Gerber Reservoir is also part of the water-management system, but its location was previously occupied by a marsh rather than by a lake. Other lakes relevant to the welfare of suckers include those lying behind five mainstem dams that, except for Keno Dam, incorporate hydroelectric production facilities (Figure 1-3, Table 3-1). The last in the sequence of mainstem dams, Iron Gate Dam, provides reregulation capability for the main stem of the Klamath River as explained below.

Of the lakes used for storage and routing, Upper Klamath Lake, Clear Lake, and Gerber Reservoir support the largest populations of listed suckers (see Chapter 6 for a detailed treatment of the suckers), and these three lakes have been the main focus of ecological and limnological analysis related to the welfare of suckers. Upper Klamath Lake has been studied especially intensively because it potentially would support the largest population of suckers and shows the greatest number of environmental problems, as indicated by episodic mass mortality of adults and probable hardships in all life-history stages. Clear Lake and Gerber Reservoir afford a useful comparison with Upper Klamath Lake because the sucker populations there have not suffered mass mortality and are generally more stable than the populations of Upper Klamath Lake. The hydroelectric reservoirs on the main stem have been studied sparingly and are of less interest than other lakes from the viewpoint of listed suckers.

The lakes shown in Table 3-1 do not serve as habitat for coho salmon, which are blocked by Iron Gate Dam from entry into the upper Klamath basin. Limnological characteristics of the waters behind Iron Gate Dam are potentially important to the coho salmon, however, in that waters released from the dam have a large influence on the water-quality characteristics of the Klamath River main stem, especially near the dam. Reflecting the relative amounts of research or monitoring and the apparent ranking of lakes with respect to their importance for the

Table 3-1. Basic Information on Lakes of Upper Klamath Basin[a]

Lake Name	Size Before 1900 (acres)		Size Since 1960 (acres)		Volume[b] (acre-ft)	Mean Depth[b] (ft)	Hydraulic Residence Time[b] (days)
	Minimum	Maximum	Minimum	Maximum			
Lakes and reservoirs used for water storage and routing							
Upper Klamath[c]	78,000	111,000	56,000	67,000	603,000	9	180
Lower Klamath[d]	85,000	94,000	4,700	4,700	<20,000	<4	<70
Clear Lake[d]	15,000	15,000	8,410	25,700	527,000	20	1,600
Tule Lake[d]	55,000	110,000	9,500	13,000	50,000	4	180
Gerber Reservoir[d]	N/A	N/A	1,100	3,900	94,000	24	600
Reservoirs used for power production							
Keno[e]	N/A	N/A	2,470	2,470	18,500	7	6
J.C. Boyle[e]	N/A	N/A	420	420	1,700	4	1.2
Copco No. 1[e]	N/A	N/A	1,000	1,000	46,900	47	12
Copco No. 2[e]	N/A	N/A	40	40	70	2	0.02
Iron Gate[e]	N/A	N/A	950	950	58,800	62	16
Total	233,000	330,000	82,120	116,710	1,420,000	-	-

[a]Lake Ewauna, which is named on some maps, is part of the Keno impoundment; Agency Lake (Figure 1-3) is treated here as part of Upper Klamath Lake.
[b]At maximum depth. Mean depths and hydraulic residence times typically are lower than shown in table, which is based on maximum volume.
[c]From Welch and Burke 2001, Table 2-1. Current maximum corresponds to water level of 4143.3 ft above sea level. Area and volume data from USFWS (2002).
[d]From USBR 2002a, Table 4.1.
[e]From PacifiCorp 2000, pp. 2-16 to 2-17; Keno has no turbines.

endangered and threatened fishes, this chapter devotes most of its attention to Upper Klamath Lake, some to the other lakes that are used for storage and routing of water, and some to waters above Iron Gate Dam that hold non-reproducing populations of listed suckers and have the potential to affect coho downstream; the remnants of Tule Lake and Lower Klamath Lake provide little lacustrine habitat at present, but offer potential for restoration.

UPPER KLAMATH LAKE

Description

Upper Klamath Lake is the largest body of water in the Klamath basin and is one of the largest lakes in the western United States (about 140 mi^2). The lake and its drainage lie on volcanic deposits derived in part from the nearby Crater Lake caldera, which took its present form as a result of the eruption of Mount Mazama (about 6800 BP). The lake also shows a strong tectonic influence, however, as is evident from a pronounced scarp along its southwestern edge (Figure 3-1). Although Upper Klamath Lake has a very low relative depth (ratio of depth to mean diameter), it has substantial pockets of water over 20 ft deep (maximum, 31 ft at a water level of 4141.3 ft above sea level; USBR 1999 as cited in Welch and Burke 2001). The northern, southern, and eastern portions of the lake and Agency Lake, which is connected to Upper Klamath Lake and is here treated as part of it, are uniformly shallow; they offer water little deeper than 6 or 7 ft at mean summer lake elevation (4141.3 ft above sea level). Even though specific runoff for the watershed of Upper Klamath Lake is relatively low (about 300 mm/yr), the hydraulic residence time of Upper Klamath Lake is only about 6 mo because the lake is shallow (there is considerable interannual variability). The flat bathymetry of the lake also causes its surface area to be quite sensitive to changes in water level.

Before the construction of Link River Dam, which was completed in 1921, the water level of Upper Klamath Lake fluctuated within a relatively narrow range (about 3 ft), as would be expected for a natural hydrologic regime (Figure 3-2). Although irrigation was under way in the basin at that time, there was no means of using the lake for storage. Water level in the lake was determined by a lava dam at the outlet (4138 ft above sea level; USFWS 2002). Even under drought conditions, the lake level remained above the level of the natural outlet, except briefly during oscillations caused by wind (USFWS 2002).

When Link River Dam was constructed, the natural rock dam at the outlet of Upper Klamath Lake was removed so that the storage potential of the lake could be used in support of irrigation. Thus, since 1921, lake levels have varied over a range of about 6 ft rather than the natural range of about 3 ft (Figure 3-2). Drawdown of about 3 ft from the original minimum water level of the lake has occurred in years of severe water shortage (1926, 1929, 1992, and 1994). The operating range of the lake in the context of mean depth and contact between the lake and its wetlands has raised numerous questions about the environmental effects of water-level manipulations, especially under the most extreme operating conditions (USFWS 2002).

The U.S. Bureau of Reclamation (USBR 2002a) has proposed operating Upper Klamath Lake over the next 10 yr according to guidelines that reflect recent historical operating practice (Figure 3-2; Chapter 1). The open question for researchers and for the tribes and government

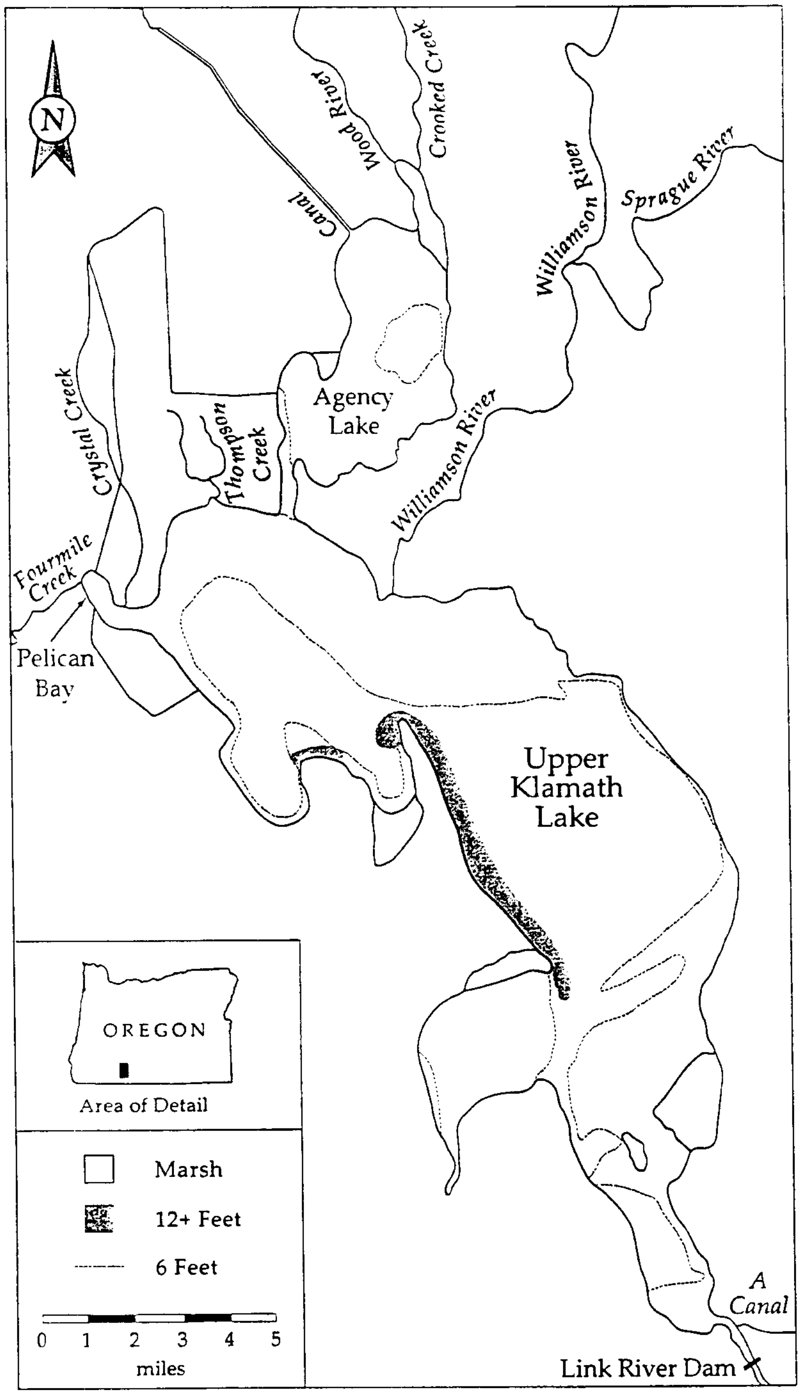


Figure 3-1. Bathymetric map of Upper Klamath Lake and Agency Lake showing depths at the mean summer lake elevation of 4141 ft above sea level. Contours are from data of U.S. Bureau of Reclamation (1999) as reported by Welch and Burke (2001). Source: Welch and Burke 2001.

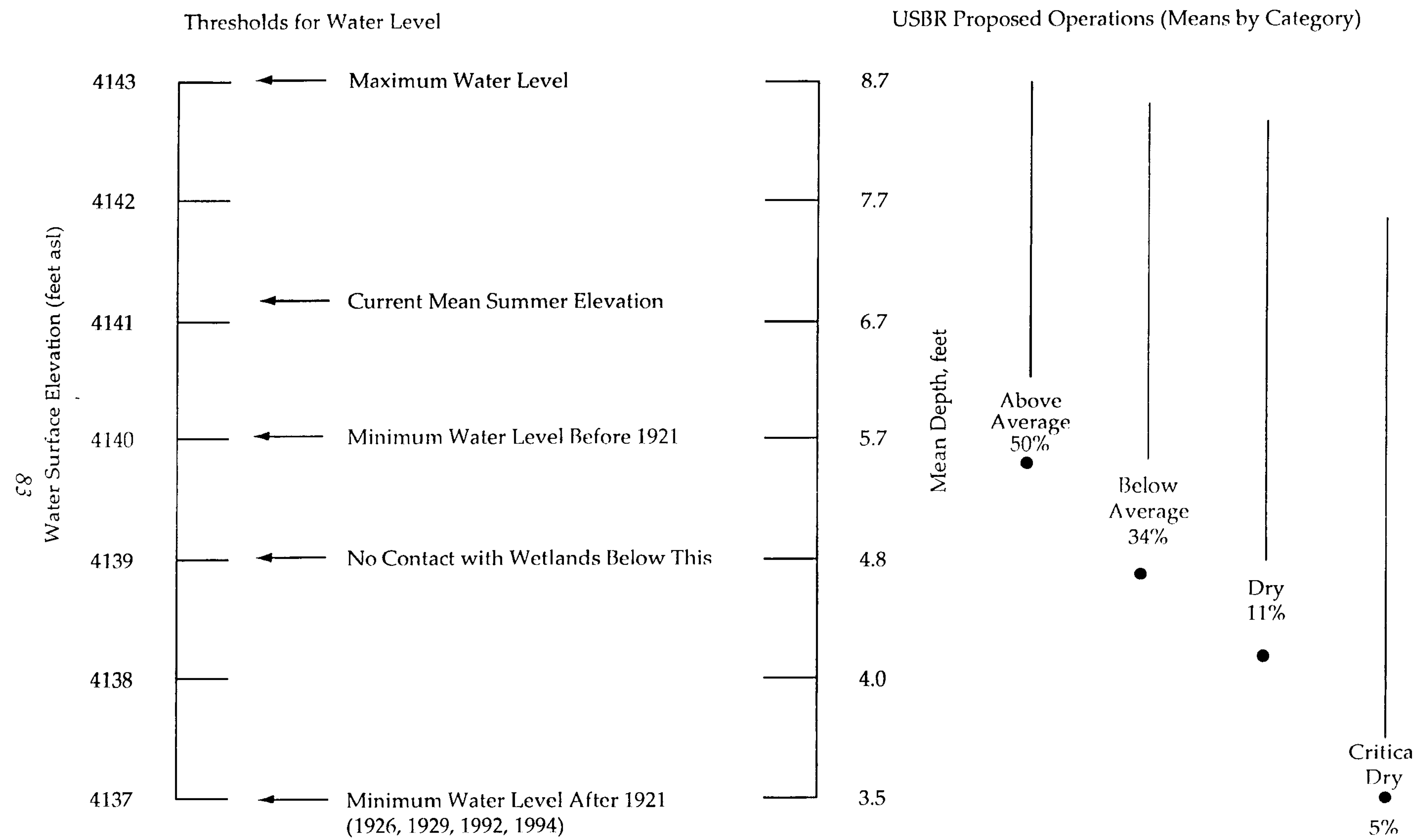


Figure 3-2. Water level of Upper Klamath Lake and mean water levels proposed by USBR for years of varying water availability. The vertical lines on the right show interannual mean operating range for an entire season (March 16-October 30). Minimums for specific years can reach below the interannual means; absolute minimums are shown as dots. Source: USBR 2002a.

agencies charged with evaluating the two endangered suckers is whether the USBR proposal for future operations is consistent with the welfare of listed suckers in Upper Klamath Lake. In a biological opinion issued in response to USBR's proposals, the U.S. Fish and Wildlife Service (USFWS 2002) has concluded that operations should involve limits on water levels that are more restrictive than those proposed by USBR. USFWS has temporarily accepted the water-level criteria proposed by USBR (2002a), but has required a revised approach to predicting water availabilities in any given year (Chapter 1).

The USBR 10-yr plan is based on a commitment of USBR not to allow Upper Klamath Lake to fall in any given year below the minimum water levels that were observed in 1990-1999 for four hydrologic categories of years and not to allow the interannual mean water levels for these categories to fall below recent interannual means (1990-1999). Figure 3-2 shows the March 16-October 30 operating range based on interannual means for each of the four hydrologic categories. The database for the definition of the categories included water years 1961-1997 (USBR 2002a, p. 39). The calculations were based on the outflow from Upper Klamath Lake for April-September. Years above the mean outflow, which is 500,400 acre-ft, are designated "above average." Those within one standard deviation below the mean are designated "below average"; the expected long-term frequency for these years is 34% (on the basis of a normal distribution). Curve-fitting was not suitable for evaluating years of lower flow, however. Two extreme years, 1992 and 1994, were designated "critical dry" and account for about 5% of the total. By difference, a fourth category, designated "dry," is defined; it accounts for about 11% of years.

For each category of years, the maximum water levels occur in the spring. Water levels typically begin relatively high as of mid-March and then rise slightly, after which they fall because of the cumulative effects of drawdown and, after June, the reduced volume of runoff (Figure 3-3). Operations for the four hydrologic categories differ most notably in their lower extremes, which occur after July. In comparison with a baseline condition, which USBR defines as lacking Klamath Project operations but with all project facilities in place, proposed operations typically produce water levels that are above the baseline between March and the end of June and below the baseline during the last half of the summer or fall (USBR 2002a).

Upper Klamath Lake receives most of its water from the Williamson River (including its largest tributary, the Sprague River) and the Wood River. Additional water sources include precipitation on the lake surface, direct drainage from smaller tributaries and marshes, and springs that bring water into the lake near or beneath the water surface. The waters of the lake have only moderate amounts of dissolved solids (interseasonal median, about 100 µS/cm) and the same is true of alkalinity (interseasonal median, about 60 mg/L as calcium carbonate). As described below, the lake is naturally eutrophic, but concentrations of nutrients in the water column may have increased over the last several decades. The fish community of the lake could be described as a diverse array of nonnative species superimposed on a previously abundant but now reduced group of native fishes, most of which are endemics (Chapter 6). The biota in general has undergone considerable change in the last few decades.

Upper Klamath Lake has several large marshes at its margins. The area of the marshes has been greatly reduced (loss of about 40,000 acres from the lake margin; USFWS 2002). The remaining marshes are most strongly connected to the lake at high water and are progressively

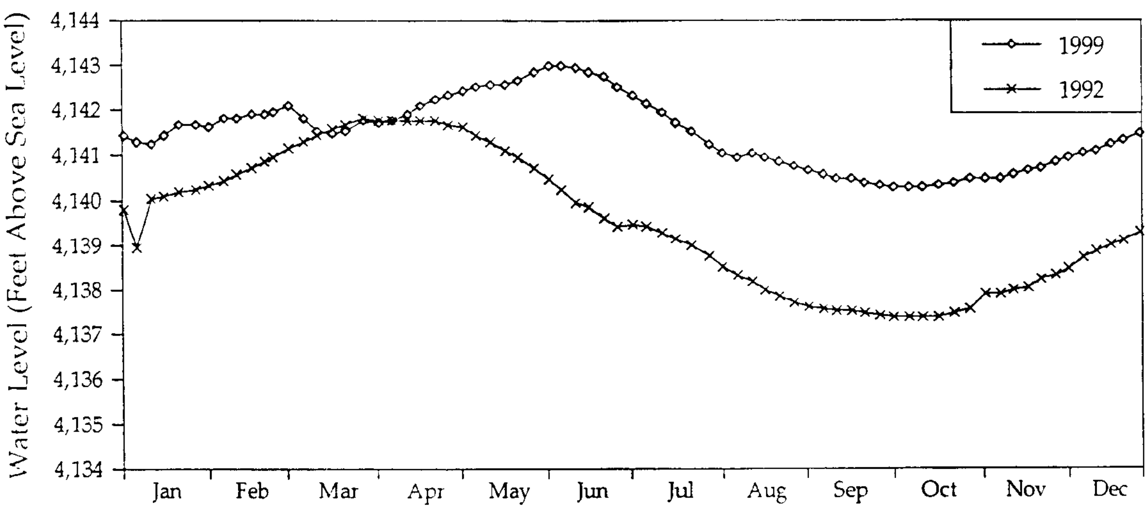


Figure 3-3. Water level in Upper Klamath Lake in year of near-average mean water level (1999) and year of extremely low water level (lowest 5%; 1992).

less connected at lower water levels down to about 4139 ft above sea level, at which point they become disconnected.

Poor water quality in Upper Klamath Lake causes mass mortality of listed suckers and may suppress the suckers' growth, reproductive success, and resistance to disease or parasitism. Potential agents of stress and death include high pH, high concentrations of ammonia, and low dissolved oxygen (USFWS 2002). Extremes in these variables are explained by the presence of dense populations of phytoplankton (primarily the cyanobacterial taxon *Aphanizomenon flos-aquae*), especially in the last half of the growing season (Kann 1998, Welch and Burke 2001). Because phytoplankton populations annually reach abundances exceeding 100 µg/L of chlorophyll *a*, the lake can be classified as hypertrophic (or, equivalently, hypereutrophic) according to standard criteria for trophic classification of lakes (OECD 1982: peak chlorophyll over 75 is hypertrophic). Hypertrophic lakes often show extremes in chemical conditions resembling those observed in Upper Klamath Lake.

The main subjects of interest with respect to Upper Klamath Lake proper (discounting the tributaries, which are dealt with in the next chapter) include factors that have been suspected by researchers or by government agencies of being potentially harmful to the endangered suckers. Where water quality is concerned, the causes of the current trophic status of the lake are of great interest, as is the current predominance of a single algal species, *Aphanizomenon flos-aquae,* in the phytoplankton. Within the suite of variables affected by trophic status, special attention must fall on pH, ammonia, and dissolved oxygen, all of which have the potential to be directly or indirectly harmful to the welfare of the endangered suckers. For all water-quality variables, associations between water level and water quality are of special interest because USBR has the potential to modify operations so as to control water level. Finally, physical habitat, especially as affected by water level, is of concern and will be dealt with here.

Nutrients and Trophic Status of Upper Klamath Lake

Nutrient limitation of phytoplankton in lakes usually is seasonal and almost always is associated with nitrogen, phosphorus, or both of these elements. Typically, phosphorus and nitrogen are readily available during winter because demand is low. In spring, the most available forms are taken up, and nutrient limitation often ensues. If the most readily available forms are available in quantities above about 10 µg/L, there is a strong implication that no limitation is occurring (e.g., Morris and Lewis 1988); at lower concentrations, nutrient limitation is possible but may be delayed by internal storage. Nutrient limitation often is relieved in the fall by deep, continuous mixing of the water column, declining irradiance, and lower metabolic rates caused by lower temperatures.

Nitrogen limitation can be defeated by some taxa of bluegreen algae (cyanobacteria) capable of fixing nitrogen (converting N_2 to NH_3). Nitrogen gas (N_2) is present in considerable quantity in water, and the overlying atmosphere acts as a large reservoir that can replenish removal of nitrogen gas by nitrogen fixation. The heterocystous bluegreen algae—which have a special cell, the heterocyst—fix nitrogen readily, although the fixation process requires high intensities of light (Lewis and Levine 1984). Heterocystous bluegreen algae do not grow well in some situations, however, for reasons that are only partly understood (Reynolds 1993). Thus, nitrogen depletion sometimes can occur without inducing growth of nitrogen fixers. Nitrogen fixers grow well in most warm, fertile waters of high pH. When phosphorus is abundant in such waters but nitrogen is scarce, nitrogen fixers have a competitive advantage and often become dominant elements of the phytoplankton. This is the situation in Upper Klamath Lake. For the phytoplankton as a whole in Upper Klamath Lake, nitrogen is limiting (see below), but *Aphanizomenon* has circumvented nitrogen limitation through nitrogen fixation and thus dominates the community.

Typically, the most effective way to control phytoplankton abundance in lakes is to restrict phosphorus supply. Restriction of nitrogen supply is not as effective, because it may lead to the development of nitrogen fixers that are able to offset restrictions in nitrogen supply. Thus, the most obvious way of attempting to control phytoplankton populations in Upper Klamath Lake is to restrict phosphorus supply. As explained below, Upper Klamath Lake presents special difficulties for strategies involving control of phosphorus.

Phosphorus in Upper Klamath Lake

The watershed of Upper Klamath Lake is geologically rich in phosphorus (Walker 2001). Springs have a median phosphorus content of about 60 µg/L as soluble reactive phosphorus, which Boyd et al. (2001, citing Walker 2001) take as an estimate of the background discharge-weighted mean phosphorus concentration. This may be an underestimate, given that springs typically have little or no particulate phosphorus or soluble organic phosphorus, both of which would be present in natural runoff from the watershed. In contrast, watersheds of granitic geology often have discharge-weighted mean total P concentrations of 20 µg/L or less (inorganic P about 5 µg/L), provided that they are not disturbed by human activity (e.g., Schindler et al. 1976, Lewis 1986).

Because background concentrations of phosphorus reaching Upper Klamath Lake are quite high, the lake probably supported dense populations of phytoplankton before land-use development. Early observations indicate that the waters were green, and thus eutrophic, at a time when water quality would have been changed little from the natural state. If, as suggested by Boyd et al. (2001), phosphorus reaching the lake would have had originally a discharge-weighted mean phosphorus concentration of about 60 μg/L, phosphorus in lake water would have been somewhat below 60 μg/L (because of sedimentation of some phosphorus) in the absence of internal loading (net increase originating from sediments). On the basis of empirical relationships between chlorophyll *a* and phosphorus (OECD 1982), the mean chlorophyll *a* in the growing season with total phosphorus at 60 μg/L would have been in the vicinity of 20 μg/L, which would have corresponded to short-term maximums of 40-60 μg/L, or about 20% of the current maximums. The concentrations of phosphorus in the lake could have been higher, however, if substantial internal loading from sediments occurred under natural conditions, in which case chlorophyll could also have been higher.

Monitoring of phosphorus entering the lake has shown that the current discharge-weighted mean phosphorus concentration in waters entering Upper Klamath Lake is near 100 μg/L, about 40% of which is considered to be anthropogenic (Boyd et al. 2001). Concentrations in the lake during spring are only about 50 μg/L (Boyd et al. 2001, Figure 2-6; there is considerable variation from year to year); the difference between the supply water and the concentrations in spring is accounted for by sedimentation of the particulate fraction of incoming phosphorus and by mechanisms that convert incoming soluble phosphorus to particulate phosphorus that can undergo sedimentation. The currently observed total phosphorus concentrations in spring, if not supplemented by any other sources, would support mean algal abundances during the growing season corresponding to chlorophyll *a* at 20 μg/L or less, according to equations developed by the Organization for Economic Co-Operation and Development (OECD 1982).

When the growing season begins (in about May), Upper Klamath Lake shows a steady rise in concentrations of total phosphorus culminating in summer concentrations of 200-300 μg/L (Boyd et al. 2001, Figure 2-6; there is considerable variation from year to year). These concentrations greatly exceed the discharge-weighted mean concentrations in inflowing water (about 100 μg/L) and also greatly exceed the concentrations in the lake during spring (about 50 μg/L, Figure 3-4). Thus, the great increase in concentrations of phosphorus during the growing season must be attributed to an internal source (sediments).

Concentrations of soluble phosphorus in sediments of Upper Klamath Lake were studied by Gahler and Sanville (1971), as reported by Bortleson and Fretwell (1993). Sediment samples taken at one location in 1968-1970 showed a median soluble phosphorus concentration in the interstitial waters of about 7000 μg/L, or about 25 times the maximum concentrations observed in the overlying lake water (another location showed less extreme deviation from lake water). Thus, for at least some portions of the lake, sediment pore waters contain substantially more soluble phosphorus than the overlying lake water and can serve as an internal source of phosphorus if the phosphorus leaves the sediments. This is a common situation in fertile lakes.

The efficiency with which phosphorus is released from sediments varies greatly according to the conditions in a particular lake. There are four potential mechanisms of release: (1) If the sediments are disturbed by wind-driven currents or by other means (organisms or

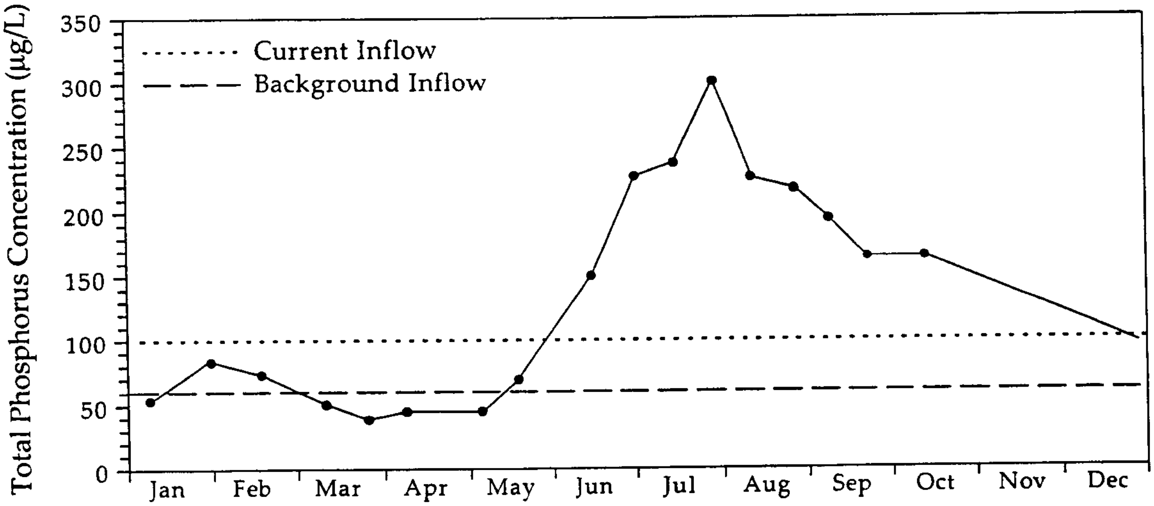


Figure 3-4. Total phosphorus concentrations in Upper Klamath Lake during 1997 (an arbitrarily chosen year) and approximate discharge-weighted mean total phosphorus for inflow for background and for current conditions. Source: data from Walker 2001.

degassing), interstitial phosphorus can be transferred to the water column simply by agitation. (2) Decrease in the redox potential (increase in availability of electrons) in the surficial sediments caused by intensive microbial respiration, as would be the case for highly organic sediment, can cause biogeochemical changes that result in accelerated release of mineralized or soluble organic phosphorus from the sediments to the overlying water, even if the sediments are immobile. (3) High pH at the sediment surface may cause release of adsorbed phosphorus from sediments, with or without agitation of sediments. (4) In shallow lakes, phytoplankton cells may, under calm conditions, sink to the sediment surface, where phosphorus is more concentrated than in the water column, and then be resuspended either by wind or by buoyancy control mechanisms after assimilating phosphorus, thus bringing phosphorus from the sediments to the water column. Internal loading in Upper Klamath Lake is caused by one or more of these four mechanisms, which are not mutually exclusive.

Chlorophyll concentrations in Upper Klamath Lake increase in parallel with concentrations of total phosphorus in the water column from May to July (Boyd et al. 2001). Thus, the data indicate that phytoplankton are assimilating an internal phosphorus load leading to an increase in their biomass. The growth process culminates in concentrations of phytoplankton chlorophyll *a* typically near or above 200 µg/L (Boyd et al. 2001). At such high abundances, phytoplankton approach the maximum sustainable biomass based on light availability (self shading) rather than nutrients (Welch and Burke 2001). The specific limit for phytoplankton biomass based on light rather than nutrients depends on physical conditions in a lake and physiological characteristics of the dominant algae (Wetzel 2001).

Because internal loading increases the phosphorus inventory of the water column in Upper Klamath Lake, thus sustaining high populations of bluegreen algae, its mechanisms are of special importance to the nutrient economy and trophic status of the lake and therefore to water-quality conditions that affect fish.

The simplest mechanism of release of phosphorus from the sediments is disturbance of the sediments. As proposed initially by Bortleson and Fretwell (1993), that mechanism is highly feasible in Upper Klamath Lake because of the lake's low relative depth (a low ratio of depth to area), which is an indication that sediments will easily be mobilized by strong winds, at least over the large expanses of shallow water. Thus, decomposition processes in the sediments may liberate phosphorus from particulate form, and this phosphorus can be transferred to the water column simply by wind-generated sediment movement. Release of gas bubbles from the sediment or invertebrate activity (bioturbation) can produce similar effects. The role of sediment movement in mobilizing phosphorus in Upper Klamath Lake is unknown, but the ability of the wind to move sediments readily over much of the lake bottom is generally acknowledged (Bortleson and Fretwell 1993).

Release of phosphorus from sediments also can occur without any movement of the sediments. If there is a substantial concentration gradient of soluble phosphorus between the sediment pore waters and the overlying water, the potential exists for diffusion of phosphorus from the pore waters to the overlying lake water and distribution of the released phosphorus by eddy diffusion or bulk mixing of the water column. The key requirements for the process include presence of a substantial concentration gradient (which exists in at least some places in Upper Klamath Lake, as indicated by the study cited above) and absence of any physical or chemical barrier to diffusion of soluble phosphorus.

It is well known that iron in the ferric state can bind phosphorus, thus restricting its movement from sediments to water (Mortimer 1941, 1942). Loss of the precipitated (ferric) iron from the surface of lake sediments occurs when sediments are anoxic for long intervals, by conversion of iron to a soluble (ferrous) state. Loss of ferric iron facilitates exchange between the sediment pore waters and the overlying water and releases phosphorus bound by ferric iron. The result can be release of large amounts of phosphorus from the sediments (internal loading). The release of phosphate from sediments caused by changes in the oxidation state of iron is most likely in lakes that show prolonged anoxia at the sediment-water interface. Unlike deeper lakes, Upper Klamath Lake does not remain stratified for the entire growing season, but rather for periods of only days or at most weeks at a time, so a key role for the redox mechanism seems less likely than it would in some other lakes, but it cannot be ruled out.

The adsorption of phosphate by ferric complexes is influenced by pH. Phosphate may pass from a sediment surface to the overlying water if the pH is high (> 8; literature reviewed by Marsden 1989), even without conversion of ferric to ferrous iron. Thus, internal loading in Upper Klamath Lake may involve iron and phosphate under oxic conditions at the sediment surface if pH is high. This mechanism is considered by some researchers to be of special importance in Upper Klamath Lake (summary in Boyd et al. 2001).

Biogeochemical mechanisms (loss of oxygen and high pH) involving release of phosphorus from sediments typically are described in terms of abiotic reactions involving iron, but there is some evidence that bacterial metabolism also accounts for binding or release of phosphorus at the sediment-water interface (Davison 1993). Bacteria also control the oxidation conditions on the sediment surface.

Phosphorus mobilization from sediments of Upper Klamath Lake also may involve direct contact between the algae and the sediments. *Aphanizomenon* contains pseudovacuoles that function as buoyancy-control mechanisms. Under some circumstances, which may coincide with nutrient deficiency, the algae may show higher specific gravity than at other times and thus show an increased tendency to sink. Because nutrients typically are more available in deep water than in shallow water, sinking, which would be notable primarily under calm conditions, can allow algae to reach nutrient reserves that otherwise are not available. In Upper Klamath Lake, a small amount of sinking could allow a substantial fraction of the algal population to have direct contact with the sediments, where phosphorus supplies are rich. Thus, algae may be mobilizing phosphorus through direct contact with the sediments (cf. Ganf and Oliver 1982).

Nitrogen in Upper Klamath Lake

The total nitrogen load to Upper Klamath Lake has been calculated for total-maximum-daily-load (TMDL) purposes as 663,000 kg/yr (Boyd et al. 2001, Walker 2001). Thus, the mass ratio of nitrogen to phosphorus for loading under present circumstances is about 3.6:1. This ratio is extreme in the sense that mass transport of nitrogen and phosphorus from watersheds to lakes typically involves mass ratios well in excess of 5:1 (OECD 1982). Although human activities tend to cause higher relative enrichment with phosphorus than with nitrogen, even disturbed watersheds typically have much higher nitrogen transport than phosphorus transport.

The ratio of nitrogen to phosphorus typically is evaluated with respect to phytoplankton growth by reference to the Redfield ratio, which is an empirically determined value for the relative amounts of nitrogen and phosphorus that are needed by phytoplankton for growth (Harris 1986). The Redfield ratio is 16:1 on a molar basis and 7.5:1 on a mass basis. In environments that show ratios far above the Redfield ratio, strong and persistent phosphorus limitation is expected. Where the reverse is true, all taxa of algae are likely to be nitrogen-limited except those capable of nitrogen fixation. Thus, where the nitrogen:phosphorus ratio is low, as it is in Upper Klamath Lake, the nutritional conditions are ideal for dominance by nitrogen-fixing bluegreen algae, such as *Aphanizomenon flos-aquae*. The fixation of nitrogen by *Aphanizomenon flos-aquae* has the effect of raising the nitrogen:phosphorus ratio by adding atmospheric nitrogen to the lake through the fixation process. While the nitrogen:phosphorus ratio still is low, a rise in this ratio due specifically to *Aphanizomenon* has increased the ability of the lake to produce algal biomass.

Explanations of Dominance by Aphanizomenon

A recent analysis showed that akinetes, which are resting cells of *Aphanizomenon flos-aquae*, are concentrated in recently accumulated sediments but not in sediments of an earlier era corresponding to predisturbance conditions (Eilers et al. 2001). Eilers et al. concluded that the strong dominance of the algal flora in Upper Klamath Lake by heterocystous bluegreen algae is a byproduct of human presence. Historical observations of phytoplankton, as summarized by

Bortleson and Fretwell (1993), are consistent with the paleolimnological conclusions. A brief overview of the chronology of observations on phytoplankton is as follows (condensed from Bortleson and Fretwell 1993): In 1906, ice from Upper Klamath Lake was deemed unsuitable for consumption because of high organic matter and green color; in 1913, summer phytoplankton samples showed diatoms dominant and bluegreen algae accounting for only 12% of cells; in 1928, water samples showed abundant algae but no dominance by bluegreens; in 1933, *Aphanizomenon* was reported for the first time but not as a dominant; in about 1939, *Aphanizomenon* was abundant but not dominant; in 1957, *Aphanizomenon* was 10 times more abundant than in 1939 but not yet overwhelmingly dominant; and in the 1960s and later, *Aphanizomenon* constituted almost a monoculture during most of the growing season.

It would be tempting to attribute the low ratio of nitrogen to phosphorus reaching Upper Klamath Lake to anthropogenic augmentation of phosphorus supply. From the TMDL mass-balance analysis, however, it is clear that Upper Klamath Lake probably had an even lower ratio of nitrogen to phosphorus in its predisturbance state (Boyd et al. 2001) because it has an unusually rich geologic source of phosphorus. Thus, nutritional conditions in Upper Klamath Lake favorable to nitrogen-fixing bluegreen algae such as *Aphanizomenon* are not new. The combination of high phosphorus concentrations under background conditions and the low ratio of nitrogen to phosphorus would have created ideal nutritional conditions for the growth of bluegreen algae before human alteration of nutrient loading, yet *Aphanizomenon* blooms appear to be a byproduct of human activity.

The conditions in Upper Klamath Lake prior to anthropogenic change could have involved some factor that prevented the population growth of bluegreen algae, even though nutrient conditions favored nitrogen-fixing algae such as *Aphanizomenon*. It has been suggested, for example, that organic acids (designated here as limnohumic acids and consisting mainly of humic and fulvic acids) present in wetland sediments are capable of chemically suppressing the growth of bluegreen algae (Eilers et al. 2001, Geiger 2001), although the phycological literature on limnohumic acids contains little indication of such effects (Jones 1998, but see also Kim and Wetzel 1993). Drainage of wetlands and hydrologic alteration in the watershed of Upper Klamath Lake probably has reduced the transfer of limnohumic acids to the lake. It is unknown, however, whether limnohumic acids or other substances derived from wetlands would have been present in sufficiently high quantities to inhibit the growth of bluegreen algae under the original conditions of the lake or why this inhibition would have been operating selectively on *Aphanizomenon*, given that other algae were abundant.

Another possibility, apparently not proposed for Upper Klamath Lake (although listed by Geiger 2001), has to do with light climate as influenced by limnohumic acids. A record from 1854 (unpublished document of the state of Oregon, as given by Martin 1997) states suggestively that the water of Upper Klamath Lake "had a dark color, and a disagreeable taste occasioned apparently by decayed tule." Limnohumic acids, which can originate in large quantities from some types of wetlands (especially those of low alkalinity), absorb light strongly at short wavelengths (Thurman 1985) and may substantially affect the light climate of phytoplankton (Jones 1998). For example, Morris et al. (1995) and Williamson et al. (1996) showed that the depth of 1% light declined from 12 m to 2 m as dissolved organic carbon (mostly limnohumic acids) increased from 2 to 10 mg/L in a series of 65 lakes of varied latitude. An increase in absorbance of such magnitude could substantially cut the amount of light reaching phytoplankton. Some diatoms are better adapted to deal photosynthetically with low light availability than most bluegreen algae (Reynolds 1984), but the high light requirement of nitrogen fixation may be even more important. Among the bluegreens, the Nostocales (including *Aphanizomenon*) have especially high light requirements (Weidner et al. 2002, Havens et al. 1998). Thus, a change in light climate rather than a change in nutrient loading or other chemical effects could have been responsible for the shift from diatoms to bluegreen algae. This is only one of several possibilities, however.

Yet another possibility has to do with biotic changes in Upper Klamath Lake. *Aphanizomenon* grows relatively slowly and so is especially vulnerable to grazing, as shown by Howarth and colleagues in marine environments (Howarth et al. 1999, Marino et al. 2002, Chan 2001; see also Ganf 1983). It is conceivable that the intensity of grazing by zooplankton on algae has been altered by the introduction of fishes that are efficient zooplanktivores. In the absence of so many efficient planktivores, zooplankton populations could have been much higher and thus capable of working selectively against *Aphanizomenon* and other nitrogen fixers. Contradicting this hypothesis is the abundance of a large and efficient zooplankton grazer, *Daphnia* (Kann 1998). In fact Kann (1998) proposes that *Daphnia* may promote *Aphanizomenon* by grazing preferentially on its competitors.

Although it seems fairly certain that *Aphanizomenon* has come into dominance in Upper Klamath Lake through human influences, the causal mechanisms of this undesirable change in phytoplankton dominance remain unclear.

Seasonal Development of Algal Biomass

Regular sampling of phytoplankton biomass at multiple stations in 1990-1998 has provided a substantial amount of information on the time course and interannual variability of biomass development of *Aphanizomenon* in Upper Klamath Lake (Kann 1998, Welch and Burke 2001). As is typical of phytoplankton populations, the phytoplankton of Upper Klamath Lake, of which over 90% is *Aphanizomenon* at peak algal abundance, shows a burst of growth in spring followed by decline. The progression of abundance is irregular, however, in that an initial period of rapid growth may be interrupted or delayed, and a period of general decline may lead to renewed growth (Figure 3-5).

The growing season for phytoplankton in Upper Klamath Lake begins generally in April. Wood et al. (1996) proposed that water temperature would show the most direct control on the rate of increase in early spring, when other conditions for growth are favorable, and thus might be a good predictor of the elapsed time between the beginning of the growing season and any particular biomass threshold that might be considered an algal bloom. This concept was investigated by Kann (1998), who showed a statistically significant association between degree days and elapsed time between the beginning of the growing season and the time coinciding with development of a specific biomass. According to Kann's analysis, days elapsed between April 1 and a biomass threshold of 10 mg/L of wet mass could be predicted with fairly high confidence ($r^2 = 0.69$) from degree days between April 1 and May 15. At the lower end of the interannual growth rate spectrum, the threshold was reached after 150 days; at the upper end, after 170 days. A relationship with lake volume in May was also tested and was suggestive but not statistically

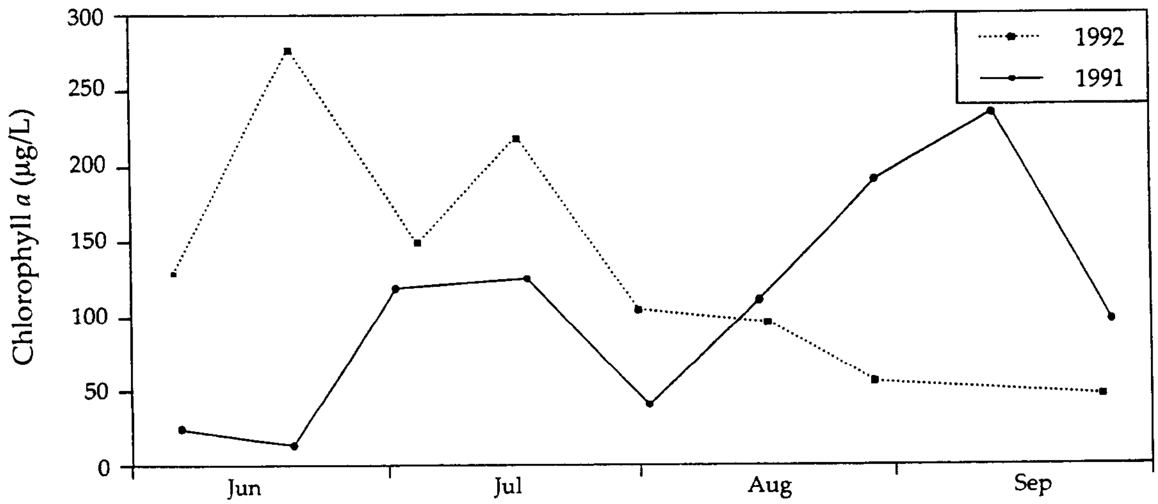


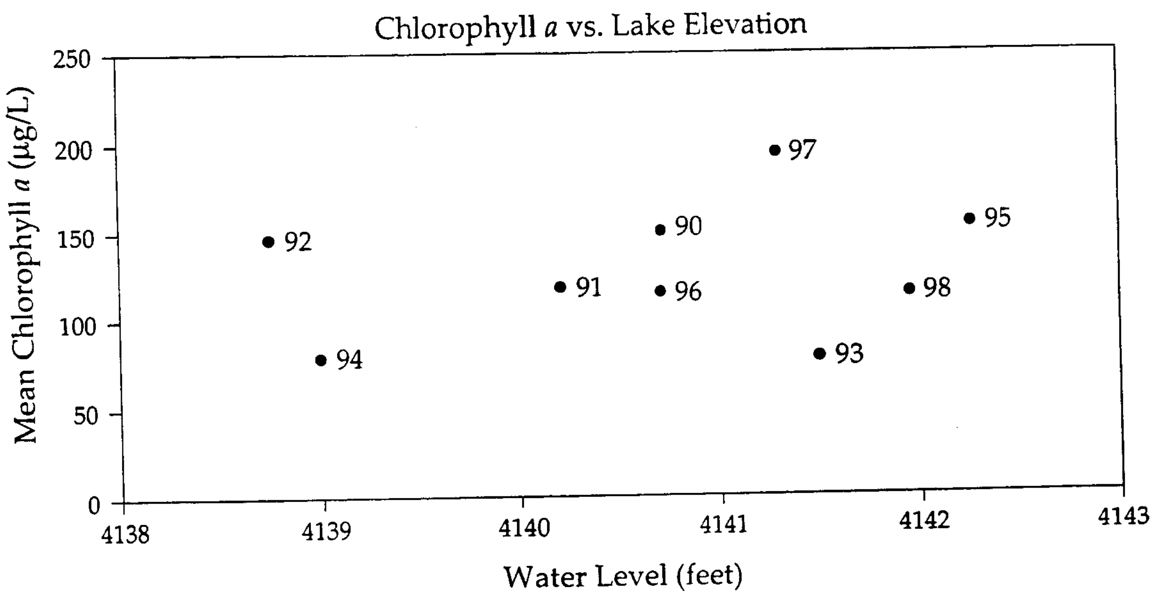
Figure 3-5. Change in chlorophyll *a* (lakewide averages, volume-weighted) over growing season for 2 consecutive years showing the potential interannual variability in development of chlorophyll maximums. Source: redrawn from Welch and Burke 2001.

significant and it depends heavily on an outlying data point for 1992, without which there is no hint of a trend related to lake volume in May. A larger dataset might show a weak but significant relationship on the basis that a lower mean depth might lead to faster warming, but interannual variation in weather introduces considerable variation not related to lake depth.

Kann (1998) and Welch and Burke (2001) have placed considerable emphasis on the relationship between water temperature and the first occurrence of a threshold biomass of *Aphanizomenon* equal to 10 mg/L of wet mass in spring. The relationship is well supported by data, but it has virtually no application to the occurrence or timing of extreme water-quality conditions. The threshold of 10 mg/L of wet mass corresponds to chlorophyll *a* at about 20-30 µg/L, which is only about 10-20% of the maximum abundance of *Aphanizomenon* as it reaches its annual peak. Although temperature influences growth in early spring, it later loses its influence because temperature stabilizes and the full development of the bloom to harmful proportions depends on other factors, as acknowledged by Welch and Burke (2001). Thus, the relationship between temperature and growth rate of *Aphanizomenon* in early spring seems to be a dead end with respect to anticipating the timing of the ultimate biomass maximums or their magnitude.

Of direct interest in connection with extremes of water-quality degradation during summer are the mean and maximum biomasses for suspended algae (primarily *Aphanizomenon*) that the lake shows in a given year. As shown in Figure 3-6, neither peak biomass nor mean biomass during the growing season has any empirical relationship with water level in Upper Klamath Lake.

Welch and Burke have modeled the abundance of *Aphanizomenon* on the basis of light availability with the assumption that nutrients are available in sufficient quantities to produce very high biomass (which is demonstrably correct). Light availability is affected by mean depth.



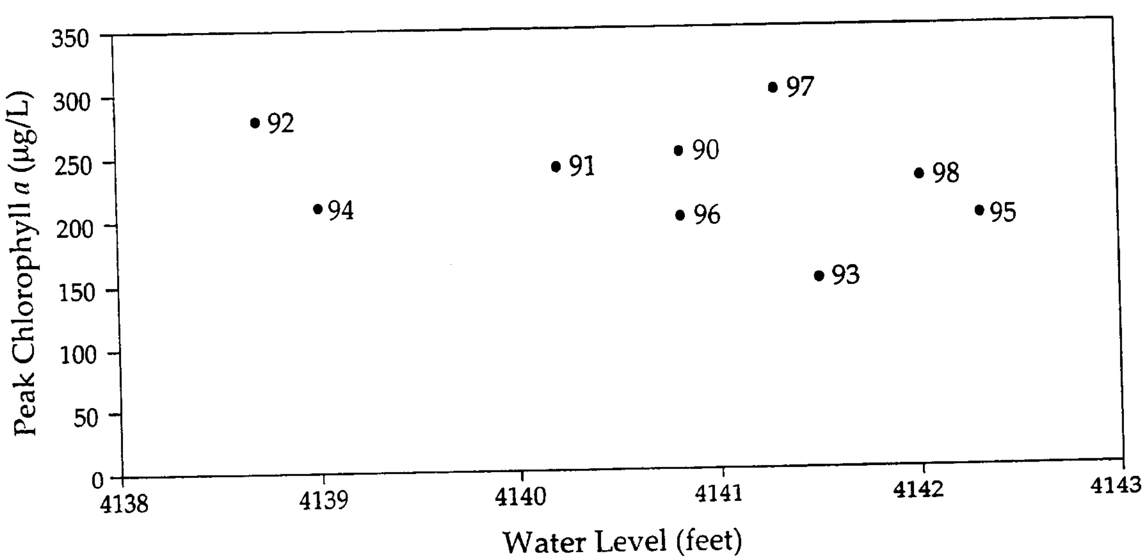


Figure 3-6. Relationship of mean chlorophyll (above) and peak chlorophyll (below) to water level in Upper Klamath Lake (median level for July and August). Source: data from Welch and Burke 2001.

As a water column gets deeper, the mean light availability for individual cells circulating in the water column declines because cells spend a higher proportion of time at greater depth, where light is less available. The modeling led Welch and Burke to conclude that maximum algal biomass of *Aphanizomenon* in Upper Klamath Lake would be quite sensitive to mean depth of the lake (Welch and Burke 2001, p. 3-15). This conclusion is inconsistent, however, with measurements of algal biomass, which show no such relationship. Thus, the model predictions are contradicted by field observations, and the latter must be given greater weight.

Modeling of the type used by Welch and Burke is useful in directing research but often produces misleading predictions because modeling usually requires various assumptions. In the case of modeling related to light, for example, the estimation of light exposure for cells must assume uniform distribution of biomass throughout the water column at all times. Because *Aphanizomenon* is capable of buoyancy regulation, it may have a nonuniform vertical distribution during calm weather. Furthermore, although Upper Klamath Lake is not stratified throughout the growing season, as deeper lakes are, it is stratified for substantial intervals during which the effective depth from the viewpoint of phytoplankton in the surface layer is less than the actual depth of the lake. Many other assumptions were necessary in modeling and could be a cause of divergence between model predictions and observations. At any rate, modeling cannot yet be used as a basis for predicting peak biomass of *Aphanizomenon* from water level in Upper Klamath Lake.

pH

Algal biomass, which typically is measured as chlorophyll concentration, is closely related to pH in Upper Klamath Lake (Kann 1998, Walker 2001). This relationship is consistent with the expected rise in pH caused by high rates of photosynthesis in aquatic environments generally (Wetzel 2001). Thus, high algal abundance sustained by light and abundant nutrients is the proximate cause of high pH during the growing season in Upper Klamath Lake.

The photosynthetically induced high pH of Upper Klamath Lake has been used in formulating a hypothesis related to the control of internal phosphorus loading in Upper Klamath Lake (Boyd et al. 2001, Walker 2001). According to this hypothesis, designated here as the pH-internal loading hypothesis, internal loading occurs primarily under oxic conditions at the sediment-water interface and involves desorption of phosphorus from ferric hydroxide complexes at the sediment-water interface through the replacement of phosphate with hydroxyl ions at high pH. Thus, high pH is proposed as a direct cause of the phosphorus enrichment of Upper Klamath Lake through internal loading during the growing season. As explained above, however, the importance of other mechanisms of internal loading cannot be ruled out, especially because internal loading substantially increases phosphorus concentrations before the lake reaches its peaks of algal abundance that are the cause of peaks in pH.

If high pH is the main cause of internal phosphorus loading, which in turn supports extremes of algal biomass in Upper Klamath Lake, internal loading might be lower if the pH of the lake were lower. Thus, external loading might be connected causally to internal loading by way of pH; this hypothesis is the basis of some recommendations in the TMDL analysis of Upper Klamath Lake (Boyd et al. 2001). The hypothesis is, however, still highly speculative.

The pH of Upper Klamath Lake also may be directly significant to fish, which can be damaged or killed by high pH. For example, Saiki et al. (1999) showed that a mean 24- to 96-h LC_{50} for the two listed sucker species in both larval and juvenile stages was 10.3-10.7. Sublethal effects would be expected below this threshold for exposures of 1 day or longer and have been demonstrated in juvenile shortnose suckers at a pH of near 9.5 (Falter and Cech 1991). Any means of suppressing extreme pH could benefit the suckers, although the degree of potential benefit is not clear. Because pH does not peak during episodes of mass mortality of suckers, however, it seems unlikely that pH contributes to mass mortality (Saiki et al. 1999). Also, because peaks of pH are transitory because of 24-h cycling of pH, impairment of fish by high pH in Upper Klamath Lake is difficult to evaluate.

As mentioned above, the immediate cause of the highest pH values in Upper Klamath Lake is photosynthesis. Furthermore, the abundance of algae, as estimated from chlorophyll *a*, is strongly correlated with pH. Thus, suppression of algal abundance would lead to a suppression of photosynthesis, which in turn would lead to a suppression of pH and, most important, elimination of the highest pH values. Kann and Smith (1999) suggested on the basis of a probabilistic analysis that a target chlorophyll *a* concentration of 100 µg/L would probably lead to a effective suppression of high pH.

The connection between pH and water level in Upper Klamath Lake has been of great interest because water level can be regulated to some degree. Welch and Burke (2001) argued on the basis of modeling that higher water levels would produce lower extremes of pH, which would potentially benefit the suckers. Their projection of pH with modeling was based on the presumption that chlorophyll *a* can be modeled in relation to water level. As mentioned above, however, observations of chlorophyll *a* in relation to water level are not as predicted by the model; there is no relationship between means or extremes of chlorophyll *a* and lake level based on monitoring during the 1990s. Thus, there is no reason to expect a relationship between pH and water level, given that pH is controlled by algal abundance. In fact, the monitoring data show no relationship between pH and water level (Figure 3-7; percentiles other than the one shown also fail to demonstrate a relationship between water level and pH). Even though they predict more favorable pH at higher lake levels, Welch and Burke (2001) acknowledge that there is no empirical relationship between pH and lake level as judged by information collected during the 1990s. The authors open the possibility of more complex relationships between lake level and pH. Any such relationship remains hypothetical, and the weight of current evidence does not support the argument that higher lake levels will mitigate problems associated with high pH.

One deficiency in the information on pH is lack of consideration of diel cycling in pH (a small amount of information is given by Martin 1997). In highly productive waters such as those of Upper Klamath Lake, pH changes extensively in a 24-h cycle; maximums occur in the afternoon hours, and minimums just before sunrise. The amplitude of pH cycles commonly exceeds 1 pH unit in fertile waters. Thus, evaluation of pH would be more complete if the pH cycle were taken into account.

Overall, pH is regulated by algae, and if the abundance of algae could be reduced, the extremes of pH could be moderated. It is likely that the abundance of algae has been increased by human actions either directly or indirectly, in which case pH under current conditions would be expected to peak substantially above the pH that was present before changes in land use in the basin. Potentially undesirable effects of high pH include direct damage to fish and amplification of internal loading, which is probably the largest source of phosphorus for Upper Klamath Lake. It is not yet clear how much harm high pH is causing suckers (especially in contrast with dissolved oxygen, for example), nor is it clear that internal loading of phosphorus, which can occur by a number of mechanisms, would be strongly suppressed by reduction in pH.

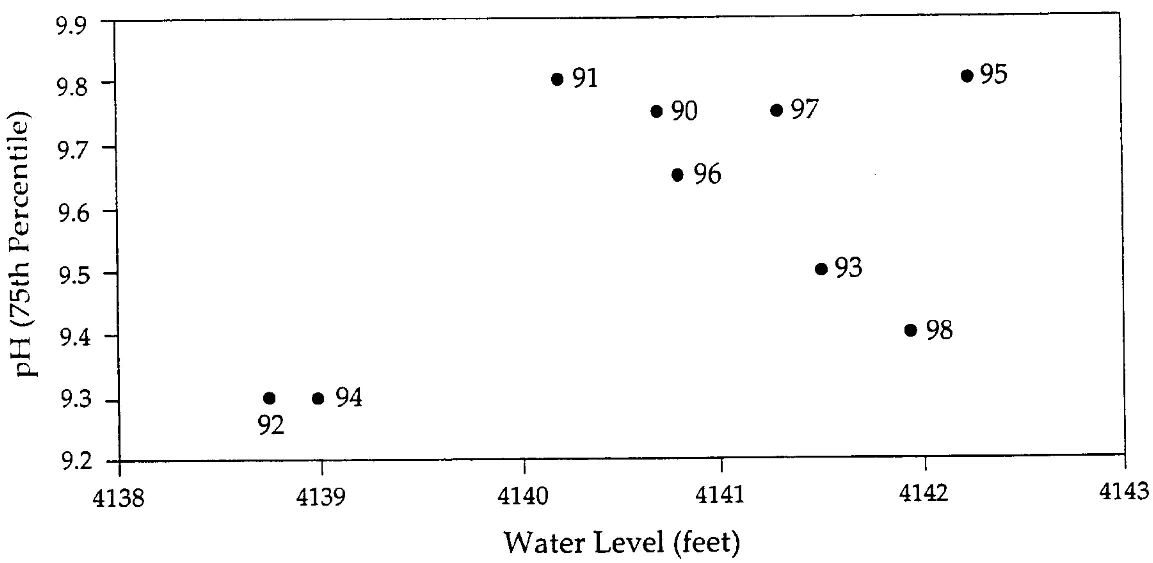


Figure 3-7. Relationship between water level (median, July and August) and pH in Upper Klamath Lake. The pH data are water-column maximum pH for 7 monitoring sites distributed across Upper Klamath Lake, shown as 75th percentile for all dates. Source: data from Welch and Burke 2001.

Ammonia

Ammonia has been proposed as a toxicant that potentially affects the endangered suckers of Upper Klamath Lake. Although ammonia is a plant nutrient with no adverse effects on organisms at very low concentrations, it is toxic at high concentrations. Toxicity typically has been associated with the unionized component of ammonia in solution. Thresholds of protection incorporated into various state regulations for warm-water aquatic life usually are in the vicinity of unionized ammonia (expressed as N) at 0.06 mg/L. Toxicity studies on the endangered suckers showed, however, that they are more tolerant of ammonia than many other species of fish (unionized ammonia LC_{50} for 24-96 h, 0.5-1.3 mg/L; Saiki et al. 1999).

Under oxic conditions, ammonia either is removed from the water column by autotrophs (which use it nutritionally) or is oxidized by nitrifying bacteria that convert it to nitrate. Thus, in the absence of a strong point source of ammonia, it is typical to have low concentrations of ammonia in inland waters that are oxic. In the absence of oxygen, however, ammonia produced by decomposition can accumulate, given that its conversion to nitrate or uptake by autotrophs does not occur under these conditions.

Upper Klamath Lake stabilizes in summer when wind speeds are low, as explained below in connection with the discussion of oxygen. At such times, ammonia accumulates in the lower water column as oxygen is depleted. Mixture of the ammonia into the entire water column could produce toxicity. Unionized ammonia seems a less likely cause of mass mortality of fish in Upper Klamath Lake than dissolved oxygen, however, because mass mortality continues after ammonia concentrations have declined (Perkins et al. 2000b), and because the suckers show relatively high tolerance to ammonia.

Dissolved Oxygen

Low concentrations of dissolved oxygen coincide with mass morality of large suckers in Upper Klamath Lake. The suckers are relatively resistant to oxygen depletion (LC_{50} 1.1 to 2.2 mg/L; Saiki et al. 1999), but their tolerance limits are exceeded under some conditions in Upper Klamath Lake (Perkins et al. 2000b). Unlike extreme pH or high ammonia concentrations, low dissolved oxygen persists for days while mortality occurs. Thus, low dissolved oxygen appears to be the direct cause of mortality.

Most lakes of middle latitude are dimictic; that is, they mix completely in spring and fall but stratify stably during summer and are covered with ice continuously or intermittently in winter. Lakes that are exceptionally shallow in relation to their area, however, are polymictic; that is, they mix many times during the growing season. The shallowest lakes, which can mix convectively at night even in the absence of wind, are designated continuous polymictic lakes (Lewis 1983). Lakes that are too deep to be mixed entirely by free convection every night (about 2-3 m; MacIntyre and Melack 1984) but too shallow to sustain stratification throughout the growing season are intermediate in the sense that they develop and sustain stratification for intervals of calm weather, especially if there is no net heat loss, and mix completely when wind strength increases or substantial heat is lost; they are called discontinuous polymictic lakes. Upper Klamath Lake is a discontinuous polymictic lake, as shown by its episodes of stratification interrupted by extended intervals of full mixing. The dynamics of water-column mixing and stratification in Upper Klamath Lake are not well documented, however, because water-quality surveys have been separated by too much time to allow resolution of the alternation between mixing and stratification in the lake.

A discontinuous polymictic lake shows alternation of the two very different conditions associated with mixed and stratified water columns. While the water column is unstratified, the lake shows minimal vertical differentiation in oxygen or other water-quality variables. When the lake stratifies, however, depletion of oxygen begins in the lower part of the water column, where contact with atmospheric oxygen is lacking and there is not enough light for photosynthesis. Because Upper Klamath Lake is highly productive, its waters have high respiratory oxygen demand that quickly leads to the depletion of oxygen in the lower water column whenever the lake is stratified (e.g., Welch and Burke 2001, Horne 2002).

An empirical relationship has been shown between relative thermal resistance to mixing (RTR, an indicator of stability) and wind velocity during July and August for Upper Klamath Lake (Welch and Burke 2001). Thus, the expectation that intermittent stability is under the control of weather has been verified for Upper Klamath Lake. Further work on the dynamics of mixing would probably be useful for understanding changes in water quality in the lake. Future work should be based on stability calculations rather than RTR, however. Stability can be calculated from morphometric data on the lake, water level, and the vertical profile of density (Wetzel and Likens 2000). Stability depends on water depth and distribution of density with depth, both of which are more irregular in Upper Klamath Lake than would be ideal for use of

RTR, which is a shortcut method of estimating stability that overlooks any changes in depth. The advantage of using true stability rather than RTR is that it may show more clearly relationships between stability and factors of interest to the analysis of mixing. The relationships already demonstrated are important, however.

Loss of stability after a period of high stability in Upper Klamath Lake is associated with low concentrations of dissolved oxygen and high concentrations of ammonia throughout the water column and with depression of algal abundances. To some extent, those changes can be understood simply as a byproduct of mass redistribution in the water column. For example, ammonia is expected to accumulate in deep water during stratification because it is a byproduct of decomposition and accumulates where oxygen is scarce or absent; it is distributed throughout the water column by destratification. Likewise, water that is depleted of oxygen near the bottom of the lake, when mixed with the upper portions of the water column, causes a decrease in oxygen concentrations in the entire water column until photosynthesis and reaeration processes at the surface combine to raise oxygen concentrations throughout the water column.

Some of the events that follow destratification in Upper Klamath Lake cannot be explained simply in terms of the redistribution of mass from a stratified water column. Concentrations of ammonia decline rather rapidly after destratification, as expected from the processes of nitrification (oxidation of ammonia to nitrate by bacteria) and autotrophic assimilation (uptake by algae). Low concentrations of dissolved oxygen, however, persist for many days rather than being offset by reaeration and photosynthesis, as might be expected. Furthermore, algal populations show substantial and prolonged decline. The prolonged decrease in oxygen appears to be the main cause of mass mortality of the endangered suckers during transition from a stratified to a fully mixed water column accompanied by the most severe decrease in dissolved oxygen (Perkins et al. 2000b). Therefore, it is important to understand why oxygen concentrations fail to recover.

The likely proximate cause of the extended decrease in oxygen concentrations after destratification is algal death. Stratification of the water column appears to produce conditions that are harmful to the algae. The mechanism of harm is still indeterminate. It could involve, for example, death of the algae that are trapped in the lower portion of the water column when stratification occurs; these algae would lack light and might be exposed to harmful chemical conditions as the lower water column becomes anoxic. Oxygen can be depleted quickly from the lower water column of Upper Klamath Lake, partly because the oxygen demand of sediments is very high (Wood 2001). One would expect that the buoyancy control of *Aphanizomenon* would allow the algae to escape these problems, but perhaps not. Alternatively, the occurrence of calm weather, which probably accompanies the development of stratification, could lead to extensive stranding of buoyant filaments of *Aphanizomenon* at the surface. This type of stranding is known to occur in dense populations of bluegreen algae. When population densities are high, the light climate is poor, and the vacuolate bluegreens often show buoyancy regulation as a means of maintaining the higher mean position in the water column, thus avoiding shading. When the water column is becalmed, however, this type of buoyancy regulation, which requires a relatively long period of adjustment, takes the filaments to the surface where they are exposed to excessive amounts of radiation (especially ultraviolet) and death results (Reynolds 1971, Horne 2002). These are merely speculations on mechanisms, however; additional research would be required to demonstrate which ones apply.

Regardless of the mechanism of algal death, it is clear that death of a substantial population of *Aphanizomenon* in Upper Klamath Lake would reduce the potential oxygen supply (by cutting off a portion of the photosynthetic capability of the water column) and would simultaneously generate a large amount of labile organic matter (as a result of the lysis of algal cells), which would raise the oxygen demand of the water column through the respiratory activities of bacteria whose growth would be stimulated by the presence of the organic matter (Figure 3-8). The extended nature of oxygen depletion suggests that it takes many days for the excess organic matter to be consumed, for the photosynthetic capacity of the lake to be regenerated, or both. In the meantime, substantial harm can occur to endangered suckers because oxygen concentrations remain low. An important practical question is whether the episodes of low dissolved oxygen throughout the water column are related to water level. Empirical evidence indicates that no such association exists, as shown Figure 3-8 (other locations and percentiles also lack a pattern). If stabilization of the water column is ultimately a danger to the fish through the induction of high algal mortality followed by loss of considerable oxygen from the entire water column, conditions leading to high stability would be least favorable to fish (Figure 3-9). Other factors being equal, deeper water columns are more stable, as acknowledged by Welch and Burke (2001); that is, one might expect higher water levels to produce greater mortality than lower water levels. However, given the complicating influence of numerous factors, including weather, associations between depth and extremes of oxygen concentrations may be too variable to detect. At any rate, there is no evidence based on oxygen that favors higher water levels over lower water levels as judged from information collected during the 1990s.

Highly productive lakes may show depletion of oxygen under ice during winter. Photosynthesis typically is weak in winter because of low irradiance and the effects of ice cover and snow on light transmission. Under winter conditions, even though respiration rates are suppressed by low temperature, dissolved oxygen can be completely depleted, and this can lead to the death of fish (winterkill). If all other factors are equal, a shallower lake is more likely to show winterkill than a deeper lake because a deeper lake has larger oxygen reserves and less respiration per unit volume than a shallower lake. Other factors are also important, however, including especially the duration of the period of ice cover and the presence of refugia, such as springs or tributaries, that move oxygen to selected locations where fish may find oxygen.

Welch and Burke (2001) and USFWS (2002) have noted risk to the endangered suckers through increased potential for winterkill when the lake is severely drawn down, as it is in dry and critical dry years. No winter mortality has been observed, however, even though the period of observation includes 2 yr that have shown more severe drawdown than any other years in the last 40 yr of record. Sparse data on oxygen under ice do not indicate depletion (USFWS 2002), but much more information is needed. Analogies that Welch and Burke (2001) have shown with studies done elsewhere may be unreliable because of differences in the duration of ice cover and other factors that make comparisons problematic. On a hypothetical basis, winter fish kill seems more likely when the lake is drawn down than when it is not, but winter fish kill may not occur at all, in which case water level is not an issue within the operating ranges of the 1990s. Measurements of oxygen concentrations under ice cover would shed additional light on this issue.

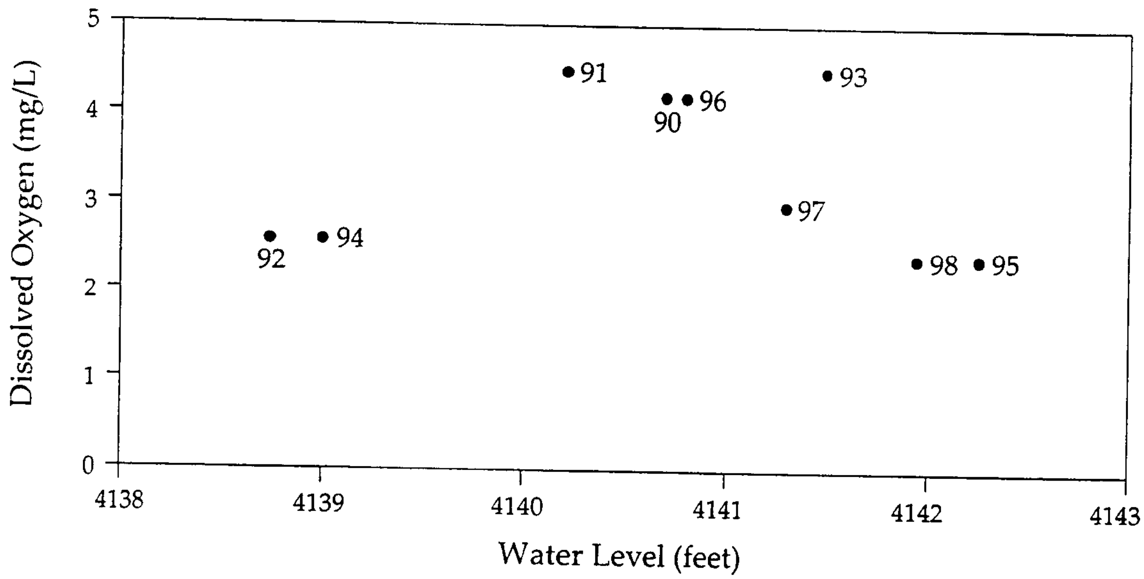


Figure 3-8. Relationship between water level (median, July and August) and dissolved oxygen in the water column of Upper Klamath Lake. Oxygen data are given as 75th percentile of minimums for all sampling dates in a given year at three sampling sites in the northern part of lake, which is considered to be especially important as habitat for large suckers. Source: data from Welch and Burke 2001.

Overview of Water Quality in Upper Klamath Lake

Poor water quality causes the mass mortality of the two endangered sucker species of Upper Klamath Lake and may also cause other, more subtle kinds of harm. The diagnosis and remediation of mechanisms leading to mass mortality or stress of fish require knowledge of the causal connections between human activity and poor water quality. Researchers working on both fish and water quality in the upper Klamath basin have worked out some causal connections (Table 3-2) but in other cases have not yet succeeded in establishing cause-effect relationships. There are two critical sets of causal connections related to water quality: (1) connection of human activity with high phytoplankton biomass and dominance of *Aphanizomenon* in Upper Klamath Lake, and (2) connection of high phytoplankton abundance with chemical conditions that could harm fish.

High phytoplankton biomass has, according to the hypothesis (external phosphorus-loading hypothesis) underlying the TMDL analysis of Boyd et al. (2001), occurred through augmentation of phosphorus loading of Upper Klamath Lake, mostly by nonpoint sources or through weakening of natural interception processes that occur in wetlands or riparian zones. There are, however, two major problems with this hypothesis (Figure 3-10). First, the anthropogenic augmentation of external loading is sufficient to account for only about 40% of the total load; the main factor accounting for very high phosphorus concentrations at present

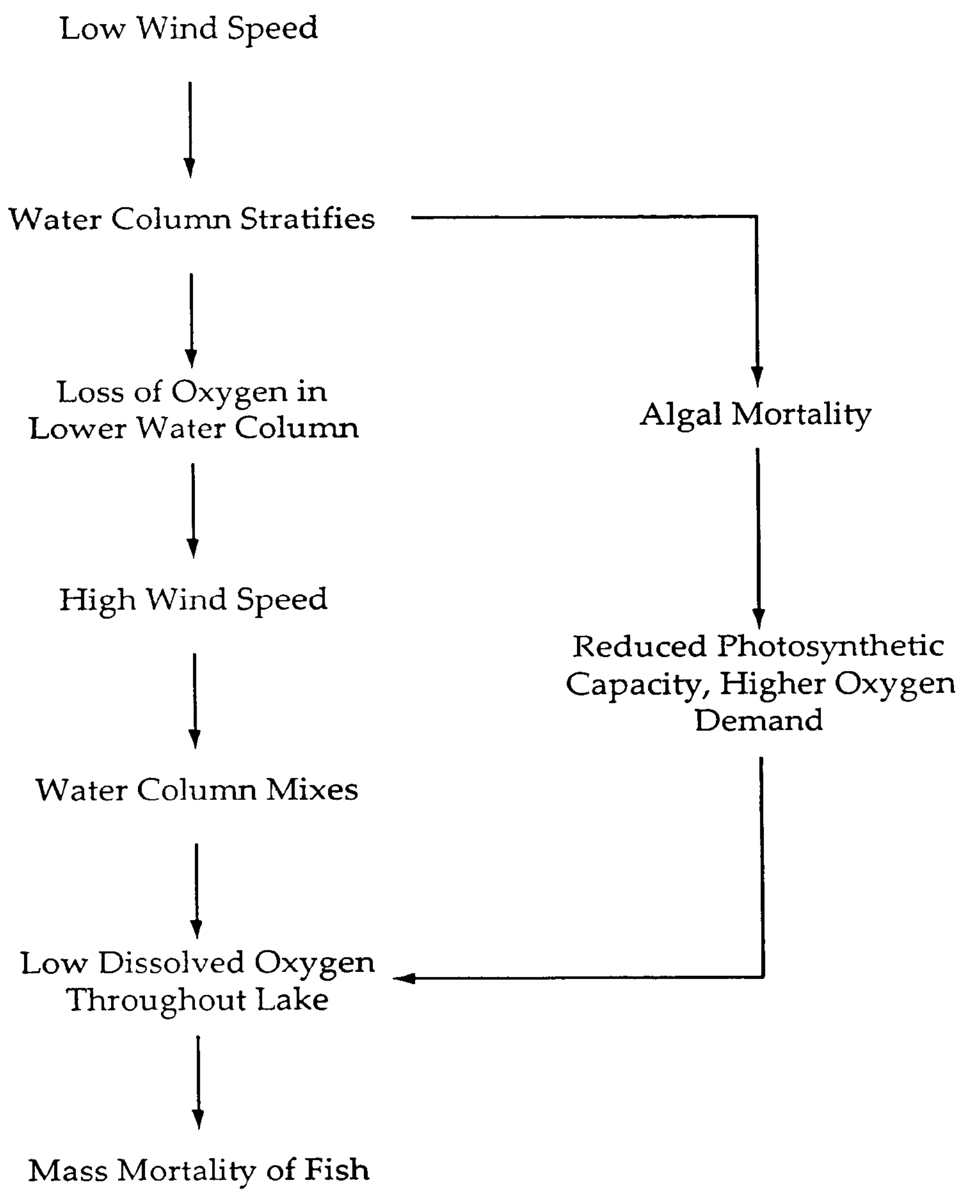


Figure 3-9. Probable cause of low dissolved oxygen throughout the water column of Upper Klamath Lake during the growing season leading to mass mortality of fish.

is internal loading rather than external loading. The pH-internal loading hypothesis proposes, however, a mechanism by which a 40% increase in external load could have produced a much larger increase in internal load. According to this line of thinking, the increase in external load

Table 3-2. Status of Various Hypotheses Related to Water Quality of Upper Klamath Lake

Hypothesis	Status
Algal abundance as measured by chlorophyll is positively related to total phosphorus in the water column	Well supported
Algal biomass as measured by chlorophyll is positively related to daytime pH	Well supported
Rate of early-spring development of biomass is positively related to rate of warming in the water column	Well supported
Rate of early-spring phytoplankton growth is inversely related to lake volume	Relationship weak or absent
Mean growing-season average algal biomass is inversely related to lake depth	Inconsistent with field data
Peak algal abundance is inversely related to lake depth	Inconsistent with field data
A large amount of phosphorus in the water column during the growing season originates in sediments (internal loading)	Well supported
pH is the main control on internal loading of phosphorus	Not resolved yet
Interception of anthropogenic phosphorus from the watershed will reduce algal abundance in the lake	Uncertain; unlikely
Lake water level is inversely related to pH	Inconsistent with field data

raised the maximum algal abundances enough to increase the maximum pH during the growing season, which in turn greatly augmented internal loading by facilitating the desorption of phosphate from iron hydroxide floc on the sediment surface. It is also possible, however, that internal loading, which can occur by several mechanisms, always has been large enough to saturate algal demand, as suggested by the steady nature of internal loading beginning early in the growing season, before pH reaches its peak. A second weakness in the external phosphorus-loading hypothesis is that it fails to explain why *Aphanizomenon* has become dominant. Nutritional conditions seem to have been favorable for *Aphanizomenon* (or other nitrogen fixers) before land-use changes in the watershed because of an inherently low nitrogen:phosphorus ratio in the lake.

Because of the two major unresolved issues for the external phosphorus-loading hypothesis, alternate hypotheses are still worthy of consideration. One, shown in Figure 3-10, is based not on phosphorus enrichment, but rather on changes in the limnohumic acid content of the lake, which is likely to have been quite high in waters emanating from the extensive wetlands

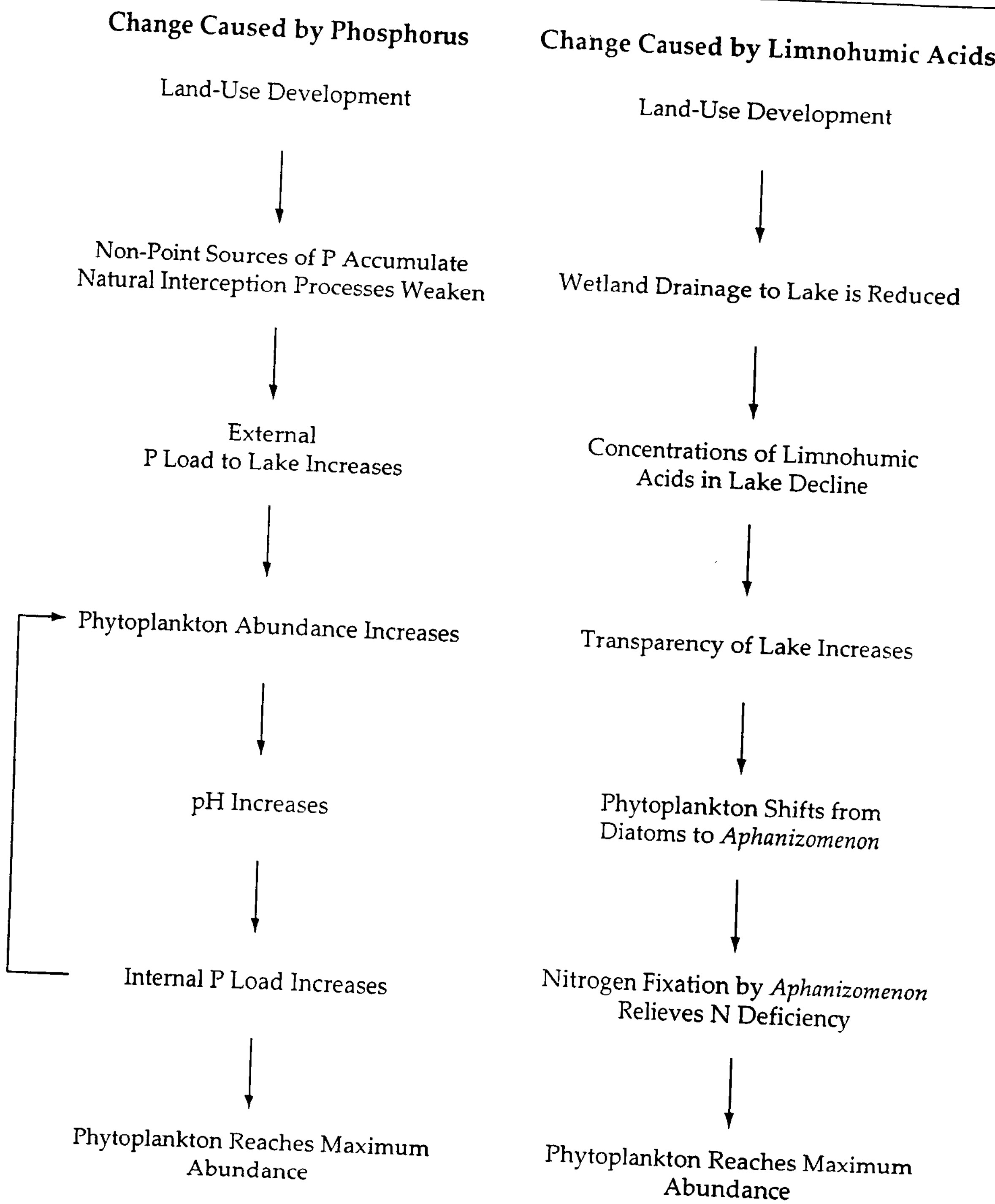


Figure 3-10. Two contrasting hypotheses that may explain connections between human activity and high abundances of phytoplankton in Upper Klamath Lake.

around Upper Klamath Lake. The hypothesis proposes that the basic cause of change in water quality of the lake is reduction in the supply of limnohumic acids to the lake, with a consequent increase in transparency or possibly even a decrease in inhibitory effects (toxicity of the acids to algae). Released from suppression by weak light availability or chemical inhibition, *Aphanizomenon* became more abundant in the lake. Unlike the diatoms that preceded it, *Aphanizomenon* was able to offset the low nitrogen:phosphorus ratio of the lake by nitrogen fixation, thus allowing algal growth for the first time to take full advantage of the abundant phosphorus supplies and produce the very high algal abundances that are now characteristic of the lake. The advantage of this hypothesis is that it accounts simultaneously for the change in community composition of phytoplankton and for an increase in biomass. The key factor causing major changes in the lake was, according to this hypothesis, drainage or hydrologic alteration of wetlands, rather than increase in external phosphorus loading.

Figure 3-11 shows causes leading from high algal abundance to water-quality conditions potentially harmful to fish. High abundance of phytoplankton produces high pH, which can be directly harmful to fish. Although the connection of phytoplankton abundance to high pH is well verified, the amount of harm to fish that it causes is still a matter of speculation. A second factor is episodic stratification of the water column, which leads to oxygen deficits in the bottom portion of the water column and appears to cause algal mortality. Mixing caused by windy weather brings oxygen-poor water to the surface, along with ammonia. The importance of ammonia in mass mortality is probably not great, but it could be harmful in more subtle ways to fish. Low oxygen that results from mixing probably is prolonged by algal death and probably is the main reason for mass mortality of fish.

Potential for Improvement of Water Quality in Upper Klamath Lake

Two proposals have been made for actions that would improve the water quality of Upper Klamath Lake. Both presume, with substantial scientific support, that an improvement of water quality in Upper Klamath Lake will require suppression of algal abundance. The first proposal, which could be implemented immediately, is for maintenance of water levels in Upper Klamath Lake exceeding levels that have been characteristic of the recent historical past. The second proposal, which deals more with long-term improvement, is for reduction in the anthropogenic component of external phosphorus loading of Upper Klamath Lake.

Higher water levels have been proposed in recent biological opinions for operation of Upper Klamath Lake (USFWS 2001, 2002). USFWS makes a number of kinds of arguments for higher water levels, while noting that empirical evidence of a connection between lake level and water quality is "weak" (USFWS 2001, p. 51). One of the arguments is that higher water levels will improve water quality in Upper Klamath Lake. As shown by the preceding review of available evidence, there is no scientific support for the proposition that higher water levels correspond to better water quality in Upper Klamath Lake. For example, mean and maximum abundances of algae, which are the driving force behind poor water quality, show no indication of a relationship with water level. USFWS acknowledges that no relationship has yet been demonstrated, but it argues that a complex, multivariate relationship may exist but not yet be evident. For example, as noted by USFWS and others (Welch and Burke 2001), an effect of

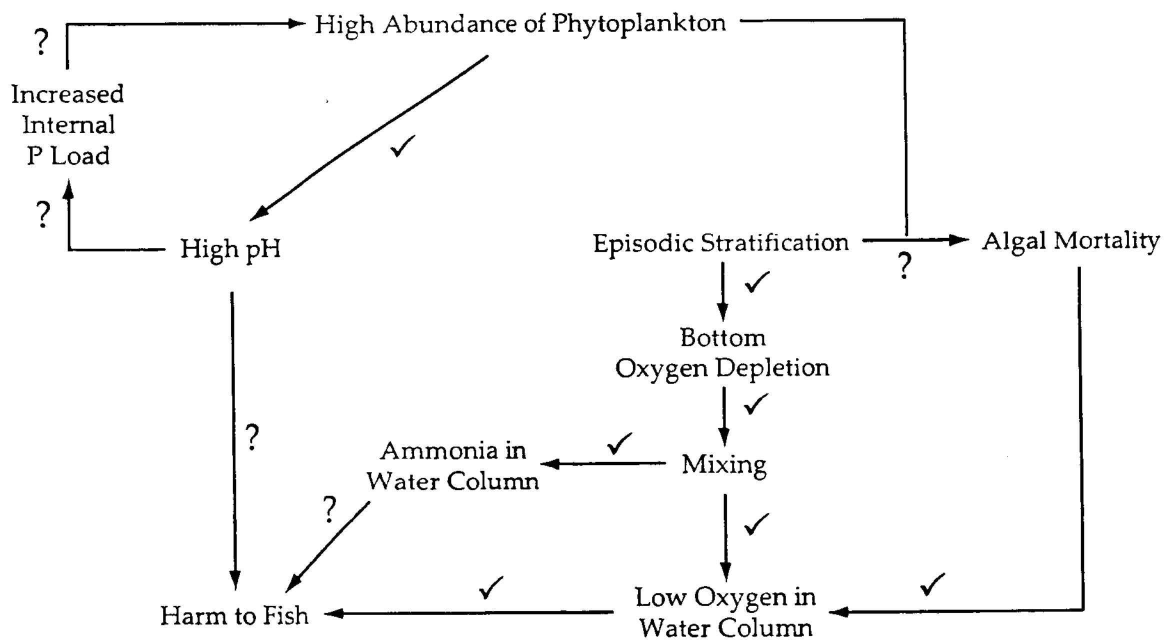


Figure 3-11. Potential (?) and demonstrated (✓) causal connections between high abundance of phytoplankton and harm to fish through poor water-quality conditions.

water level on water quality could be contingent on water-column stability, which in turn is under the influence of weather. Other multivariate relationships could be proposed that involve water level as one of several factors explaining the water-quality conditions in a given year. This line of argument leads to the conclusion that water-quality conditions may be explained in the future (after further study) by a suite of variables that include water level, but it also suggests that the influence of water level is too weak to be discerned without consideration of other variables.

The potential usefulness to management of a complex mechanism involving water level as a covariate would be low even if it could be demonstrated. Furthermore, the mode of influence of water level as one of a suite of variables affecting water quality would not necessarily work in the direction of water-quality improvement at higher water levels. For example, as indicated in the foregoing text, higher water level promotes water-column stability, which appears to be the principal means by which water-quality conditions for mass mortality develop in Upper Klamath Lake. All things considered, water level cannot now be managed with confidence for control of water quality.

The second proposal, which is for long-term improvement of water quality through reduction in external phosphorus loading, has been favored by many and is the main recommendation related to water quality of Upper Klamath Lake in a recent TMDL analysis (Boyd et al. 2001). The proposal has three weaknesses: one related to the feasibility of intercepting substantial load, a second related to the internal-load effects of reducing external load, and a third involving the role of increased phosphorus loading in sustaining large algal populations under current conditions.

The TMDL proposal is for reduction of external phosphorus by about 40%. Because the current anthropogenic load is about 40% of the total, the proposal is to return the external phosphorus loading of Upper Klamath Lake to background conditions. Only about 1% of the anthropogenic loading is from point sources (wastewater treatment plants: Boyd et al. 2001). Interception of point-source loads is technically feasible, but interception of nonpoint-source loads, although approachable through best-management practices, is more problematic in that it would require major changes in agricultural practice and other types of land use. Even a reduction of 20% would be ambitious and potentially infeasible in view of the association between non-point sources and privately held lands.

Even a reduction of 40% in total external phosphorus loading would probably be ineffectual without suppression of internal phosphorus loading, given that internal phosphorus loading is very large for Upper Klamath Lake. The authors of the TMDL study have anticipated this problem. Invoking the pH-internal loading hypothesis as described above, they anticipate that a reduction in external loading will result in lower extremes of pH, which in turn will reduce internal loading, thus providing magnified benefits. This is a highly speculative proposition, however. Because soluble phosphorus is available in quantity even at the end of the growing season, it appears that internal loading is sufficient to supersaturate the needs of algae for phosphorus. Furthermore, a pH reduction, if it did occur, might or might not be sufficient to shut off internal loading related to high pH. Finally, high pH is only one mechanism by which phosphorus is mobilized from sediments; other mechanisms would remain as they are and could easily be sufficient to provide the internal loads necessary to generate the high phytoplankton biomass observed in the lake. Thus, reduction of external load as proposed in the TMDL document has results that are quite uncertain.

A third problem with the phosphorus-reduction strategy is that the high abundances of phytoplankton in Upper Klamath Lake may have not become established because of external phosphorus loading, but rather because of other changes in the lake. A drastic decrease in mobilization of limnohumic acid alteration of wetlands and hydrology, for example, fits historical observations more satisfactorily than a phosphorus-based hypothesis, given that Upper Klamath Lake apparently has always had the very low nitrogen:phosphorus ratios that set the stage for dominance by a nitrogen fixer, such as *Aphanizomenon*. The data suggest that other factors were holding back the nitrogen fixers and that human activity reversed or modified one of them, producing the current dominance of *Aphanizomenon*. *Aphanizomenon*, once established, could generate higher abundances than nonfixing algae because of its ability to offset nitrogen deficiency in the water. Thus, the key to improving water quality may be to suppress *Aphanizomenon*.

Restoration of limnohumic acids to the lake would be the most obvious way of restoring any beneficial effects that limnohumic acids might have had before land-use development of the upper Klamath basin watershed. Restoration of wetlands is under way and could increase transport of limnohumic acids to the lake. Although justified in large part by an attempt to intercept nutrients, these programs could have beneficial effects on limnohumic acid supply. One discouraging aspect of restoring limnohumic acid transport to the lake, however, is that many of the wetland sediments surrounding the lake that would have been perhaps the richest source of limnohumic acids have disappeared through oxidation after dewatering. Furthermore, restoration of limnohumic acid supply would require not just restoration of wetlands but also extensive rerouting of water through wetlands, with attendant loss of water through evapotranspiration. Nevertheless, this option is virtually unstudied and deserves more attention. It could be compatible with nutrient-removal strategies justified by improvements in water quality of streams.

Current proposals for improvement of water quality in Upper Klamath Lake, even if implemented fully, cannot be counted on to achieve the desired improvements in water quality. Thus, it would be unjustified to rely heavily on future improvements in the water quality of Upper Klamath Lake as a means of increasing the viability of the sucker populations.

Oxygenation as a Management Tool

The possibility that oxygenation of deep water could be used as a means of reducing mass mortality of endangered suckers in Upper Klamath Lake has been mentioned by USFWS in its biological opinion (2002; see also Martin 1997). An engineering study of the possibility is already available (Horne 2002). Because of the size of Upper Klamath Lake and the speed with which it can become anoxic toward the bottom of the water column during episodes of stratification, it is unlikely that oxygenation could be used in preventing low concentrations of dissolved oxygen from developing in the lower water column during stagnation or in restoring oxygen when the water column mixes at depressed oxygen concentrations. Even so, it is conceivable that oxygenation could be used in such a way as to provide specific refuge zones to which the endangered suckers would be attracted when they experience stress due to low dissolved oxygen. Of particular interest would be the adult suckers, which cluster in specific locations (USFWS 2002).

It is doubtful that the potential for aeration to reduce mass mortality of large suckers can be developed entirely from calculations and estimations. Pilot testing for proof of concept seems well justified for the near future. Potential success of this approach is uncertain, however, in that use of oxygenation specifically to create refugia in large lakes apparently does not appear in the literature on oxygenation.

CLEAR LAKE

Clear Lake was created in 1910 at the location of a smaller natural lake and associated marsh on the Lost River (Figure 3-12). One purpose for the creation of the reservoir was to allow storage of runoff for irrigation of lands below the dam. An additional purpose was to promote evaporative loss of water that otherwise would flow to Tule Lake and Lower Klamath Lake, which were intended for dewatering to allow agricultural development. In addition to high evaporative losses associated with its low mean depth, Clear Lake has extensive seepage losses.

Clear Lake is divided into east and west lobes that are separated by a ridge; the dam is on the east lobe. Willow Creek, a tributary of Clear Lake, is critical to the sucker populations, which appear to rely primarily or even exclusively on this tributary for spawning. The lands

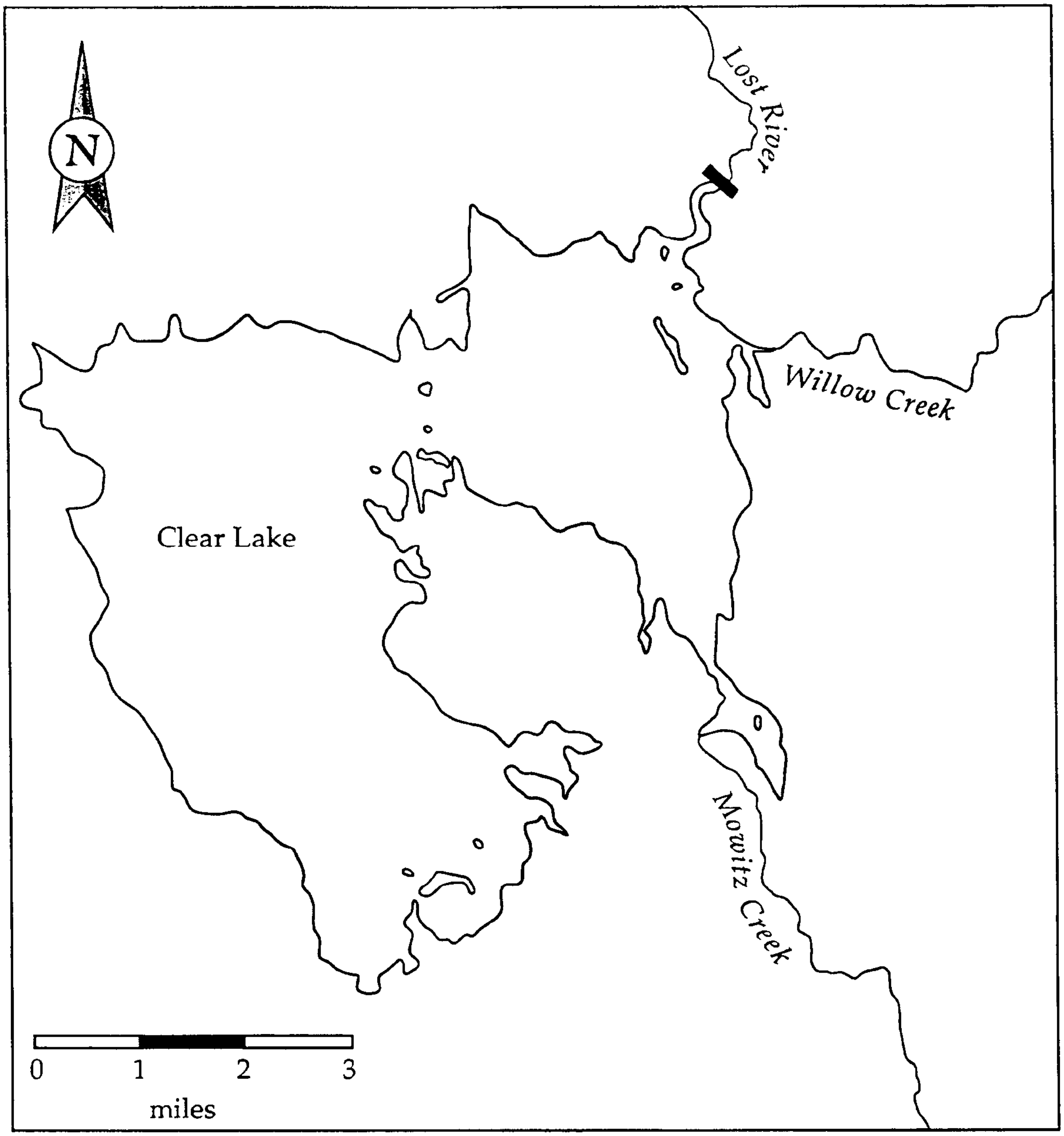


Figure 3-12. Map of Clear Lake.

surrounding Clear Lake are not under intensive agricultural use. The area surrounding the reservoir consists primarily of Clear Lake National Wildlife Refuge, and the watershed above the lake is largely encompassed by the Modoc National Forest.

Although Clear Lake would store as much as 527,000 acre-ft at its maximum height, which corresponds to a lake area of 25,000 acres (USBR 2000a), its average area has been close to 21,000 acres, which corresponds to a storage of about 167,000 acre-ft and a mean depth of 8 ft

(USBR 2002a, USBR 1994); it has never reached maximum storage. Average annual inflow is 117,000 acre-ft, which suggests a mean hydraulic residence time of 1-2 yr (computed from input and volume). Clear Lake is similar to Upper Klamath Lake in being shallow in relation to its area. It differs from Upper Klamath Lake in its considerably longer hydraulic residence time and its very low output of water relative to input. One other important feature, which has to do with water management, is the high interannual and interseasonal variation in storage volume of Clear Lake, which corresponds to great variations in area and mean depth (USBR 1994).

Clear Lake contains both shortnose and Lost River suckers (USFWS 2002). Both species show evidence of stability and ecological success in Clear Lake, as indicated by diverse age structure and high abundance (USFWS 2002, USBR 1994; Chapter 5). Interannual variations in the welfare of the populations have been scrutinized, however, because of questions related to the maximum permissible drawdown of the reservoir in a dry year or in a succession of dry years. Monitoring of water quality and condition of fish in 1991-1995 provided a good opportunity to evaluate extreme drawdown because the water level in 1992 declined to its lowest point since the drought of the 1930s.

Although water-quality records collected in 1991-1995 (USBR 1994, Hicks 2002) are useful, the breadth of information that is available for Clear Lake is much narrower than that of Upper Klamath Lake. Apparently, there has been no sampling for phytoplankton or for nutrients that would allow comparisons with Upper Klamath Lake. Observations suggest that Clear Lake has far lower population densities of phytoplankton than Upper Klamath Lake; there is no evidence of massive blooms of bluegreen algae, for example. Aquatic macrophytic vegetation like that found in Upper Klamath Lake is virtually absent from Clear Lake because of its wide range of water levels.

The water column of Clear Lake typically has a turbid appearance suggestive of fine inorganic particulate material that is continually suspended by wind-generated currents (USBR 1994). The transparency of the lake has been measured only sporadically. During 1992, when water levels were exceptionally low, Secchi depths ranged from 0.1 to 0.4 m, which indicated extremely low penetration of irradiance in the lake (M. Buettner, USBR, personal communication, 23 January 2003). In more typical years, transparency is low but not nearly at the extreme of 1992 (for example, June 1989, 0.4-1.5 m across 24 stations; M. Buettner, USBR, personal communication, 23 January 2003). Although Clear Lake is generally characterized as allowing less light penetration than Upper Klamath Lake, the scanty data on light penetration that are available suggest that the transparencies may fall within the same range for the two lakes (for example, see Kann 1998 for data on Upper Klamath Lake). Because transparency may be related to the welfare of sucker larvae through predation, which may be more pronounced in transparent waters, further study of this subject seems warranted.

In 1991-1995, recording sensors were used for measuring temperature, specific conductance, pH, and dissolved oxygen; vertical profiles also were taken for these variables. Although interpretation of the records is complicated by occasional malfunction of the sensors, which is characteristic of this type of data collection, the overall results are useful. The temperature record indicates that the lake is unstratified; if it does stratify, it does so only sporadically over the deepest water (near the dam). The pH varies seasonally but does not reach the extremes observed in Upper Klamath Lake, presumably because high rates of algal photosynthesis, the driving force behind extreme pH in Upper Klamath Lake, are not characteristic of Clear Lake (USBR 1994). The oxygen data indicate that the lake does not show episodes of strong oxygen depletion like those in Upper Klamath Lake. One incident of oxygen concentration as low as 1 mg/L near the dam apparently was associated with drainage of the east lobe of the reservoir during 1992 as the lake was drawn down to the extremes of that year. Monitoring under ice showed concentrations of oxygen near saturation, even during an interval of especially long ice cover during 1992, a year of very low water level (USBR 1994).

Mass mortality of suckers in Clear Lake is unknown. Loss of fish occurs through the dam but does not appear to be seriously decreasing the populations. The populations were studied for signs of stress during the dry year of 1992. Although mortality was not observed, there were several indicators of stress, including higher rates of parasitism and poor body condition. These indicators disappeared quickly as water levels climbed in 1993 at the end of the drought (USBR 1994). The indications of stress associated with water levels of 1992 have served as a basis of proposed thresholds of drawdown in Clear Lake (USFWS 2002).

The potential of Clear Lake to provide information about Upper Klamath Lake has not been well exploited. The agencies have invoked Clear Lake for comparative purposes in several instances, but the background information on the reservoir is not sufficiently broad and does not extend over sufficient intervals of time to allow good comparisons. Comparative population and environmental studies in the two lakes could open up new possibilities for diagnosing mechanisms that are adversely affecting endangered suckers in Upper Klamath Lake.

GERBER RESERVOIR

Gerber Reservoir was established on Miller Creek, a tributary of the Lost River, in 1925 (Figure 1-1). The lake can store as much as 94,000 acre-ft of water but often is substantially drawn down and shows considerable interannual and intraannual variability in volume, mean depth, and area (USBR 1994, 2002b). Nevertheless, characteristic depths of Gerber Reservoir probably are substantially greater than those of Upper Klamath Lake or Clear Lake. Statistics are not readily available, but the sampling record (USBR 2002b) suggests that in most years a substantial area of the lake would have water deeper than 15 ft. Extreme drawdown occurred in 1992, when the lake was reduced to less than 1% of its maximum volume (USBR 2002b). Even under those conditions, the water near the Gerber Reservoir dam was 15 ft deep.

As might be expected, given that it is smaller and deeper than Clear Lake or Upper Klamath Lake, Gerber Reservoir shows a tendency toward stability of thermal stratification, as indicated by loss of oxygen near the bottom during summer. Stability may be interrupted by mixing, and entrainment of water through the outlet may lead to a replacement of bottom waters, which could produce changes (oxygenation, warming) similar to those expected as a consequence of mixing.

Little information is available on the water quality of Gerber Reservoir. The lake appears to have less inorganic turbidity than Clear Lake, presumably because it is deeper and smaller. *Aphanizomenon flos-aquae* probably is present and apparently creates blooms but not to the same degree of Upper Klamath Lake (USFWS 2002). *Aphanizomenon* probably fares better in this reservoir than in Clear Lake because the latter has more suspended inorganic turbidity, which shades the water column.

Information on temperature, specific conductance, pH, and dissolved oxygen was collected for the first half of the 1990s by automated monitoring and occasional vertical profiles (USBR 2002b), as was the case for Clear Lake. The pH reaches higher extremes than in Clear Lake but is less extreme than in Upper Klamath Lake. This probably reflects a gradient of algal photosynthesis across the three lakes. Dissolved oxygen in Gerber Reservoir is substantially depleted in deep water both in summer and in winter, but without any obvious effect on fish. No episodes of mass mortality of the shortnose sucker, which occupies Gerber Reservoir, have been reported. During 1992, when drawdown of the lake was severe, the lake was aerated (USFWS 2002); sampling indicated that the fish had reached suboptimal body condition during the drought. Under other circumstances, the population appears to have been stable in that it has shown no indication of stress, has preserved a diversified age structure, and has been abundant. For reasons primarily having to do with water quality, the low water levels of 1992 serve as a guideline for setting thresholds to protect the fish from stress.

LOWER KLAMATH LAKE

Lower Klamath Lake has been reduced to a marshy remnant by dewatering. It has occasional connection to the Klamath River through which it appears to receive some recruitment of young suckers, but there is no adult population. Water quality apparently has not been studied in any systematic way. Development of an adult population is unlikely unless the depth of water can be increased, which would involve incursion of the boundaries of the lake onto lands that are used for agriculture. If the lake were deepened, water quality might be adequate for support of suckers.

TULE LAKE

Tule Lake historically was very large and capable of supporting, in conjunction with the Lost River, large populations of the shortnose and Lost River suckers (Chapter 5). It has been reduced to remnants as a means of allowing agricultural use of the surrounding lands. Water reaches Tule Lake from Upper Klamath Lake or from the Lost River drainage via irrigated lands or from Clear Lake or Gerber Reservoir. Water is removed from Tule Lake (now appropriately called Tule Lake Sumps) by Pump Station D (USBR 2000a).

There are two operational sumps at Tule Lake now: 1A and 1B. In the recent past, Sump 1B has been much less likely to hold adult suckers than Sump 1A; it is shallower and has shown a higher rate of sedimentation than Sump 1A. It also appears to have worse water quality than Sump 1A. Sump 1B is being manipulated by USFWS for increase of marshland in the Tule Lake basin.

Some water-quality information is available on Tule Lake through monitoring during the 1990s (USBR 2001a) and fish have been sampled (Chapters 5 and 6). It appears that the sucker population consists of a few hundred individuals, including shortnose and Lost River suckers, and that these favor specific portions of Sump 1A (the "doughnut hole" or a location in the northwest corner) that presumably provide more favorable conditions than the surrounding area.

Monitoring of Sump 1A has not shown any incidence of strongly decreased oxygen concentrations or extremely high pH, as would be the case in Upper Klamath Lake (USBR 2001a). These adverse conditions may occur in Sump 1B, however. The fish of Tule Lake, although not very abundant, appear to be in excellent body condition, and this suggests they are not experiencing stress.

Suckers migrate from Tule Lake Sumps; migration terminates on the Lost River at the Anderson Rose Diversion Dam (USFWS 2002, Appendix C), in the vicinity of which spawning is known to occur. Water-quality conditions there for spawning appear to be acceptable (USBR 2001a). Larvae are produced but apparently are not passing into the subadult and adult stages.

From the water-quality perspective, it appears that the Tule Lake population is potentially closer to survival conditions than the Upper Klamath Lake population. An unresolved mystery, however, is the fate of larvae. It is not clear whether water quality prevents the larvae from maturing, or if other factors are responsible for their loss.

Sedimentation threatens the apparently good conditions for adults in Sump 1A. Without aggressive management, the favorable portion of Sump 1A may become progressively less favorable in the future.

RESERVOIRS OF THE MAIN STEM

There are five mainstem reservoirs (Table 3-1); because Copco 2 is extremely small, it generally does not receive independent consideration. The composite residence time of water in the mainstem reservoirs, which extend about 64 mi from Link River Dam to Iron Gate Dam, averages about 1 mo. At moderately low flow (for example, 1000 cfs), hydraulic residence time is close to 2 mo; and at moderately high flow (such as 6000 cfs), it is close to 10 days. Thus, some of the processes that would make these lakes distinctive from each other and from their source waters are not expressed because of the relatively rapid movement of water through the system.

The main source of water for the mainstem reservoirs is Upper Klamath Lake, but it is not the only source. Agricultural returns and drainage water enter the system upstream of the Keno Dam (Figure 1-2) by way of the Klamath Strait Drain (about 400 cfs, summer) and the Lost River Channel (about 200-1500 cfs, fall and winter). In addition, cold springs provide about 225 cfs all year at a point just below the J.C. Boyle Dam; and two tributaries, Spencer Creek and Shovel Creek, provide 30-300 cfs to J.C. Boyle Reservoir and Copco Reservoir. Fall Creek and Jenny Creek provide 60-600 cfs to Iron Gate Reservoir. During the wet months, sources other than the Link River, which brings water from Upper Klamath Lake, provide about one-third of the total flow reaching Iron Gate Dam; in midsummer, these sources may account for up to 50% of the total water reaching Iron Gate Dam (PacifiCorp 2000, Figure 2-7). Thus, source waters of diverse quality influence the quality of water in the reservoirs. The waters of Upper Klamath Lake often bring large amounts of algal biomass to the upper end of the system, along with large amounts of soluble and total phosphorus. When Upper Klamath Lake is experiencing senescence of its algal population, the entering waters also may have low concentrations of dissolved oxygen and an abundance of decomposing organic matter. Irrigation tailwater and other drainage would carry abundant nutrients and could carry organic matter but would probably lack substantial amounts of algae. Spring waters and tributary waters would be the coolest and cleanest of the water sources.

The reservoirs differ physically in several ways that are likely to influence water quality. Keno Reservoir and J.C. Boyle Reservoir are shallow and have the lowest hydraulic residence times. Physically, they resemble rivers more than lakes. In each, the water is pooled at the lower end and may run swiftly at the upper end, thus potentially benefiting from reaeration (gas exchange). The two lower reservoirs are much deeper and have hydraulic residence times that are short on an absolute scale but much longer than those of the two upper reservoirs.

None of the reservoirs has very deep withdrawal. Thus, for the two reservoirs that support stable stratification (Copco and Iron Gate), withdrawals reflect the characteristics mostly of epilimnetic (surface) water, although their withdrawal cone may extend a short distance into the hypolimnetic (deep) zone at times (Deas 2000). For example, the temperature of water leaving Iron Gate Dam during midsummer, when the hypolimnion has a temperature of about 6°C, reaches 22-23°C (PacifiCorp 2000, Figure 4-5; Deas 2000, Figure 6.5) because the powerhouse withdrawal is at about 12 m depth when the lake is full. For Copco, withdrawal is at about 6 m when the lake is full. Thus, cold hypolimnetic water of the two deepest reservoirs tends to be much more static hydraulically than the upper water column during the stratification season, as would be the case in a natural lake of similar depth; the main withdrawal occurs by way of the epilimnion. A small withdrawal (about 50 cfs) for the Iron Gate Hatchery does occur from the hypolimnion at Iron Gate Reservoir, however.

The quality of water in the reservoirs and leaving the reservoir system has been studied many times by numerous parties dating back to the 1970s. PacifiCorp has sponsored a number of studies in conjunction with its Federal Energy Regulatory Commission (FERC) licensing and other regulatory requirements, and USBR has sponsored studies of water quality because of its oversight responsibilities for the Klamath Project. The city of Klamath Falls has also studied water quality, particularly in the upper end of the system, and the Oregon Department of Environmental Quality has studied and analyzed water quality from the viewpoint of fisheries. Other information is available from the U.S. Geological Survey, the U.S. Army Corps of Engineers, and the North Coast Regional Water Quality Control Board. In its consultation document on FERC relicensing, PacifiCorp (2000) provides an overview of the monitoring programs.

Monitoring to date provides useful information but shows several deficiencies. Most of the monitoring has been limited to water-quality variables that can be measured with meters (temperature, pH, specific conductance, and dissolved oxygen). There is much less information on nutrients, total phytoplankton abundance, phytoplankton composition, total organic matter, and other important variables. Thus, interpretations are necessarily limited in scope. Also, there have been few efforts to synthesize and interpret the data, most of which exist merely as archives. Hanna and Campbell (2000) have modeled temperature and dissolved oxygen in the reservoirs. The temperature modeling is useful for planning, but the oxygen modeling fails to incorporate primary production, which could be important. Deas (2000) has done extensive modeling for Iron Gate Reservoir that is especially useful for temperature and dissolved oxygen. A full, system-level understanding of the reservoirs is not yet available, however.

During the cool months (October or November through May), all the lakes are isothermal and appear to mix with sufficient vigor to remain almost uniform chemically (see, for example,

Figure 3-13). During the warm season, there may be substantial differences in temperature and water quality with depth. Keno Reservoir and J.C. Boyle Reservoir are not deep enough to sustain thermal stratification during summer. They may stabilize briefly, however, in which case oxygen may be depleted from deep water (see Figure 3-14), but such depletions probably are interrupted by episodes of mixing. Copco and Iron Gate reservoirs, in contrast, stratify stably on a seasonal basis. Thus, the water near the bottom of these two reservoirs can be classified as hypolimnetic and has a much lower temperature than that of the upper water column. As expected, oxygen is depleted in the hypolimnion of both lakes. Although the rate of oxygen depletion varies across years (Deas 2000), both reservoirs apparently have an anoxic hypolimnion for as much as 4 or 5 mo beginning in the last half of summer.

Periodic episodes of severe oxygen depletion may occur in the upper two reservoirs. One such event appears to have occurred in 2001, when the entire water column of Keno Reservoir became hypoxic or anoxic (Figure 3-15). It is not known how often such an event occurs. Because no mass mortality of fish in the reservoirs have been recorded, it is possible that the fish under these circumstances seek inflowing water of high oxygen concentration to sustain them until the episode dissipates.

Although the reservoirs receive abundant supplies of algae from Upper Klamath Lake, they do not appear to sustain such high rates of algal growth as Upper Klamath Lake, as indicated by comparisons of pH. Upper Klamath Lake shows extremes of pH extending above 10, but such extremes are not characteristic of the reservoirs. For example, monitoring of Copco, Iron Gate, and J.C. Boyle reservoirs in 1996-1998 by PacifiCorp showed the highest pH to be about 10.0, and even this was quite unusual (PacifiCorp 2000, Figure 4-10). More recent data are similar in this respect (Table 3-3).

Concentrations of phosphorus (means) tend to be about the same in the mainstem reservoirs as in Upper Klamath Lake. There is ample phosphorus in available form for stimulation of phytoplankton growth, but it is not clear whether a net accumulation or a net loss of phytoplankton biomass occurs in the reservoirs because information on phytoplankton biomass shows some internal inconsistencies. Observations from the field suggest that substantial blooms of *Aphanizomenon* occur in both Copco and Iron Gate reservoirs (USFWS 2002). This would not be surprising, given the strong seeding of these reservoirs with *Aphanizomenon* from Upper Klamath Lake and the presence of large amounts of nutrients. Although the residence times for the two large reservoirs are not great enough to allow the establishment of large populations of algae starting from a very small inoculum, a large inoculum could double several times over the duration of residence in the two reservoirs and thus generate a bloom. Alternatively, a bloom could simply be transferred from Upper Klamath Lake. The difficulty with the observations, however, is that they are not confirmed by monitoring data in 2000 and 2001. For both of those years, analysis of chlorophyll *a* showed abundances of algae ranging from low to high but not extreme in the sense of Upper Klamath Lake (Table 3-3). There are several possible explanations. Field reports might be biased by appearance of some algae at the surface while underlying populations are not extraordinarily high. There could be something wrong with the chlorophyll analyses, or perhaps large blooms occur very seldom. These matters are unresolved.

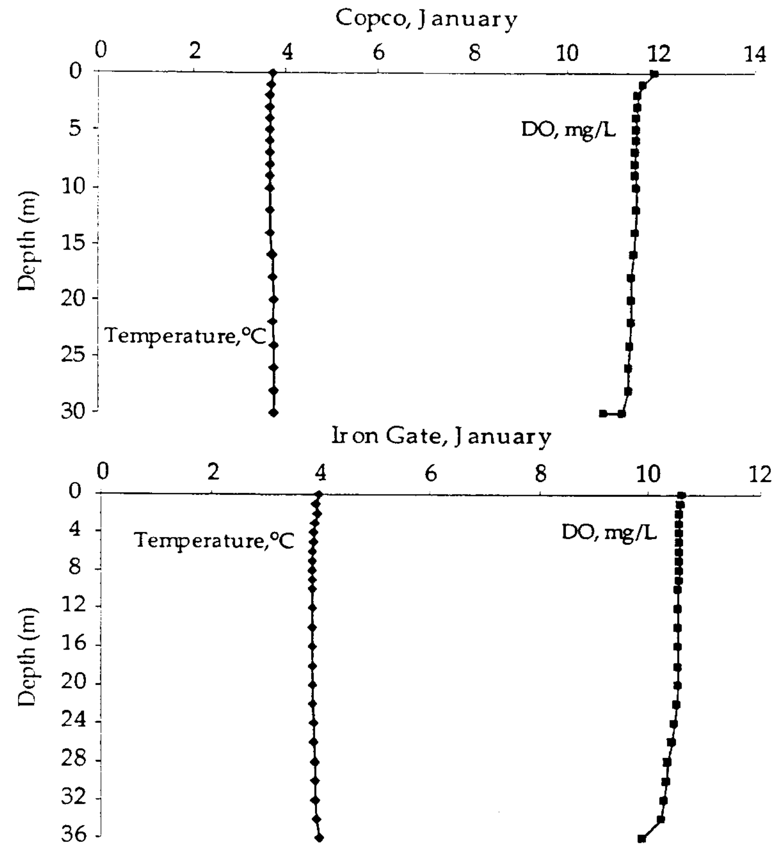


Figure 3-13. Water temperature and dissolved oxygen (DO) in Copco and Iron Gate Reservoirs, January 2000. Source: data from USBR 2003.

One special concern with respect to coho salmon and other salmonids in the Klamath River main stem is the condition of water as it leaves Iron Gate Dam. Oxygen concentrations below Iron Gate Dam are seasonally below saturation but generally exceed 75% of saturation (Deas 2000), have a temperature that reflects surface waters in the lakes, and have lower concentrations of nutrients and algae than would be typical of Upper Klamath Lake. Because there is some question about the consistency of data on algae, however, no firm conclusions are possible about the export of *Aphanizomenon* to the main stem via Iron Gate Dam.

It appears that the upper two reservoirs have the poorest water quality, as judged from concentrations of nutrients and dissolved oxygen. The two lower reservoirs, although they develop anoxia in deep waters during summer, maintain better water quality than the upper two reservoirs in their surface waters. The major question of *Aphanizomenon* blooms in the system seems unresolved because of internal inconsistencies in the data. In general, the water-quality environment seems to be comparable with or slightly better than that of Upper Klamath Lake in

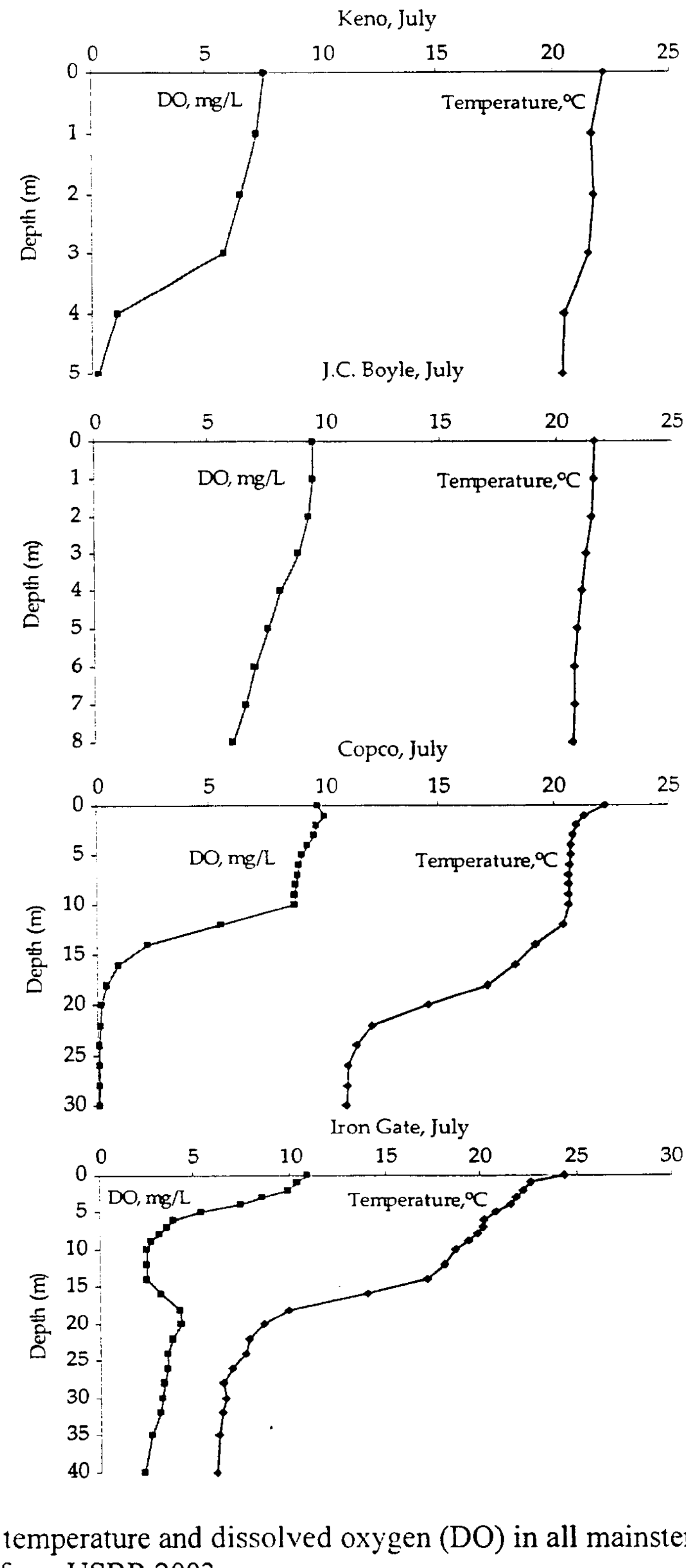


Figure 3-14. Water temperature and dissolved oxygen (DO) in all mainstem reservoirs, July 2000. Source: data from USBR 2003.

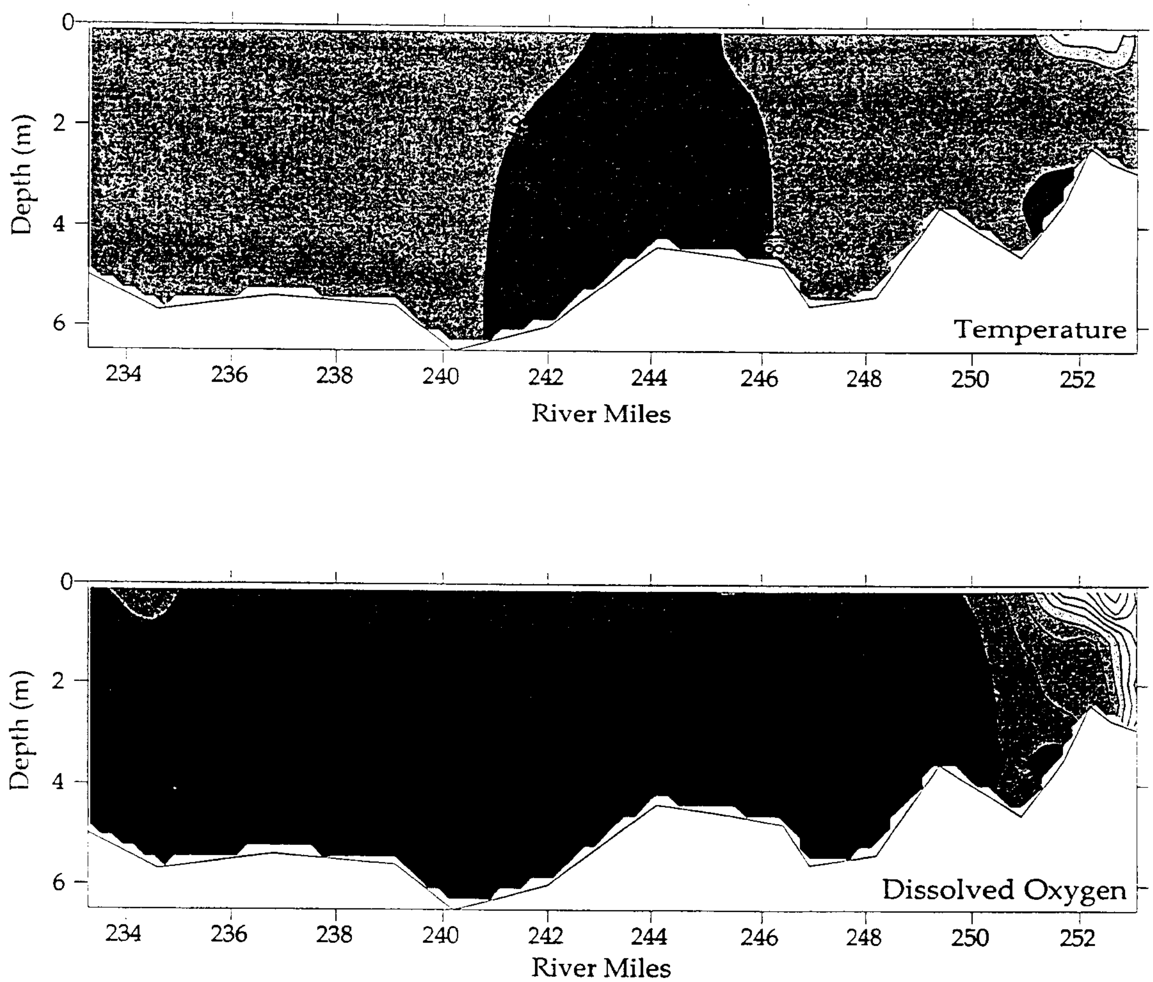


Figure 3-15. Longitudinal transect data on Keno Reservoir (Lake Ewauna), 13-14 August 2001. Isolines indicate temperature at 1°C intervals (top panel, increasing from 18°C) and dissolved oxygen at intervals of 1 mg/L (bottom panel, increasing from 1 mg/L). Darker tones indicate lower temperature or lower dissolved oxygen; the darkest zone on the bottom panel indicates concentrations of dissolved oxygen below 1 mg/L, i.e., without or almost without oxygen. Source: data from USBR.

the two upper reservoirs, which may have very low dissolved oxygen but do not seem to have the pH extremes that Upper Klamath Lake does. The two lower reservoirs appear to have better quality overall than the two upper reservoirs, although their deep waters are essentially uninhabitable for fish during the summer months because of their lack of oxygen. More synthetic work on the reservoirs is needed.

Table 3-3. Summary of Grab-Sample Data for Surface Waters in the Mainstem Reservoir System, 2001[a]

Location		pH	Concentration, μg/L NH_4^+-N	NO_3^--N	SRP	Total P[b]	Chlorophyll *a* 2001	Chlorophyll *a* 2000
Keno (1 m)	Mean	7.50	1080	80	160	390	62	-
	Max	8.82	1220	90	240	730	-	-
J.C. Boyle (1 m)	Mean	7.31	190	1120	250	260	50	5
	Max	7.86	260	1760	290	450	-	20
Copco (1 m)	Mean	7.91	90	620	150	280	5	10
	Max	8.90	130	880	220	560	-	31
Iron Gate (1m)	Mean	8.28	260	370	160	180	5	11
	Max	9.45	260	630	280	410	-	46
Below Iron Gate	Mean	7.87	80	980	170	190	4	-
(0.5 m)	Max	8.68	90	1710	210	360	-	-

[a]N = 4 in most cases (monthly, June-September); N = 1 for chlorophyll in 2001 (July); additional chlorophyll data for 2000 (N = 6) are shown for three of the reservoirs. Chlorophyll shown at concentrations below about 20 μg/L is only a rough approximation because of limitations on analytical sensitivity.
[b]Total P less than SRP (soluble reactive P) for some dates.
Sources: USBR 2003; PacifiCorp, unpublished data, 2001.

CONCLUSIONS

1. Water-quality conditions in Upper Klamath Lake are harmful to the endangered suckers. Mass mortality of large fish is caused by episodes of low dissolved oxygen throughout the water column. Very high pH and high concentrations of ammonia, although more transitory than the episodes of low dissolved oxygen, may be important agents of stress that affect the health and body condition of the fish.
2. Poor water quality in Upper Klamath Lake is caused by very high abundances of phytoplankton, which is dominated by *Aphanizomenon flos-aquae*, a nitrogen fixer. Suppression of the abundance of *Aphanizomenon* is essential to the improvement of water quality.
3. Very high abundance of *Aphanizomenon* in Upper Klamath Lake is almost certainly caused by human activities, but mechanisms are not clear. One hypothesis is that increased algal abundance has occurred because of an increase in phosphorus loading in the lake. An alternative hypothesis, which is more consistent with the shift in dominance to *Aphanizomenon* and with the naturally rich nutrient supply of phosphorus to the lake, is that loss of wetlands and hydrologic alterations have greatly reduced the supply of limnohumic acids to the lake. According to this untested hypothesis, loss of limnohumic acids greatly increased the transparency and may also have reduced inhibitory effects caused by the limnohumic acids. These changes allowed *Aphanizomenon* to replace diatoms as dominants in the phytoplankton. Total phytoplankton abundance then increased because of the ability of *Aphanizomenon* to offset nitrogen depletion by nitrogen fixation, which diatoms could not do.

4. Substantial evidence indicates that adverse water-quality conditions are not related to water level. Further study extended over many years may ultimately show multivariate relationships that involve water level. Control of water quality in Upper Klamath Lake by management of water level, within the range of lake levels observed during the 1990s, has no scientific basis at present.

5. Suppression of algal abundance in Upper Klamath Lake could involve drastic reduction in external phosphorus load or reintroduction of a substantial limnohumic acid supply, depending on the mechanism by which *Aphanizomenon* has become dominant. Both of these remedial actions, if undertaken on a scale sufficient to suppress the abundance of *Aphanizomenon,* could be achieved only over a period of many years and could prove to be entirely infeasible.

6. Because remediation of water quality in the near term seems very unlikely, recovery plans for the endangered suckers in the near term must take into account the potential for continued mass mortality of suckers.

7. Use of compressed air or oxygen to offset oxygen depletion near the bottom of Upper Klamath Lake has been suggested as a means of moderating mass mortality of adult suckers. Such a technique cannot be expected to offset oxygen depletion throughout the lake, but it has some potential to provide refuge zones. The endangered suckers may be particularly well suited for this type of treatment because the large suckers, which are susceptible to mass mortality, congregate in known locations.

8. Researchers have provided a great deal of useful information related to water quality of Upper Klamath Lake. Needs for additional information include studies designed to show the mechanism for *Aphanizomenon* death; physical studies, including continuous monitoring of temperature and oxygen and associated analytical and modeling work, that demonstrate more definitively the mechanisms that promote alternation of stratification and destratification during the growing season for the lake; studies of the effects of limnohumic acids on *Aphanizomenon* and of the former limnohumic acid supply to the lake; studies of diel pH cycling in the lake; and studies of water quality under ice.

9. Clear Lake and Gerber Reservoir lack extremes of pH, oxygen depletion, and algal blooms that occur in Upper Klamath Lake. Better water quality, in combination with other favorable factors given in more detail in Chapters 5 and 6, appear to explain steady recruitment, diverse age structure, and good body condition of these populations. Deterioration of body condition of the listed suckers at a time of extreme drawdown provide a rationale for the lower allowable thresholds of water level in these lakes. The lakes and their tributary spawning areas have exceptional value for protection against loss of the two endangered sucker species. Additional studies of limnological variables (and those of fish populations) have special value for use in comparison with water quality and population characteristics of suckers in Upper Klamath Lake.

10. Tule Lake, which supports suckers in good body condition but does not show evidence of successful recruitment, may have water quality that would allow recovery of this subpopulation if problems involving spawning habitat and larval survival were resolved. Lower Klamath Lake, which now lacks adult suckers, might well support a sucker population if water levels were raised.

11. Of the four major mainstem reservoirs, Keno and J.C. Boyle appear to have the poorest water quality because they are shallow, have the strongest influence from Upper Klamath Lake,

and show the least benefit of dilution by waters entering from other sources. Copco and Iron Gate reservoirs have better water quality but develop anoxia in hypolimnetic waters during summer. Water released to the Klamath main stem from Iron Gate Dam often is below 100% saturation with oxygen but seldom less than 75% of saturation and may be excessively warm in summer for salmonids because it is drawn mostly from the epilimnion. Algal populations in Iron Gate Reservoir appear not to reach the extremes that are typical of Upper Klamath Lake.